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FORMATION OF ASSOCIATIONS IN THE MAY-FLY NYMPHS *HEPTAGENIA INTERPUNCTATA* (SAY)

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Two figures

PROBLEM

While working on the life history and general behavior of *H. interpunctata*, I observed, on several occasions, what appeared to be indications of learning. These cases suggested several forms of experiments. Three different ways of testing the learning capacity of the nymphs were devised and carried out, namely, experiments on reactions to objects in their thigmotactic relations, experiments on fear reactions as results of associations with pain, and experiments on the formation of associations in feeding. A considerable amount of work has been done on the learning capacity of higher insects, but the

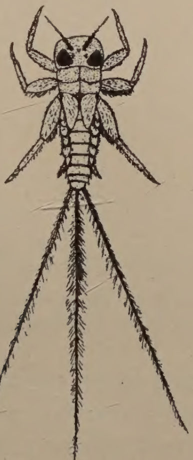

Figure 1. May-fly nymph

formation of associations in lower insects has hitherto been the subject of very few experimental investigations.

REACTIONS TO OBJECTS

Different nymphs vary greatly in their response to objects under similar conditions. Some, for instance, will go as far as 11 inches in a direct line toward a stone about one cubic inch in size, while others seem to be unaware of the object even when it is much nearer.

I experimented with 20 specimens in a large glass basin, evenly lighted and evenly colored. The nymphs were placed, one at a time, in a small glass passage, represented by AB in the diagram, within and close to one side of the large basin, and a stone a little more than one cubic inch in size was placed about a foot away from the opening of the glass tunnel.

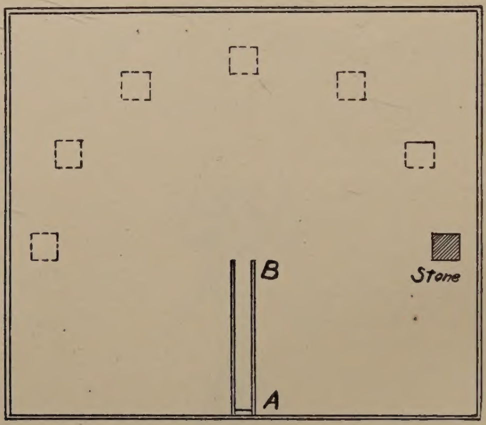

FIGURE 2. Diagram of apparatus used in the experiments on reactions to objects

The little glass tunnel was to prevent random movements. Specimens dropped into water, owing to excitement, are apt to swim about in any direction. A specimen would be carefully placed at the closed end of the passage, which was sufficiently wide to enable it to move freely forward, but which would not permit it to turn around. Slight stimulation from behind induced it to swim forward. In doing so it had ample time to get a view of the enclosure before it reached the open end of the tunnel. If the nymph, after emerging from the tunnel, did not go in a straight line in the direction of the stone, the stone would be brought closer at each trial until a distance was obtained at which the insect would make several successive straight trips to it. The stone would then be placed at the same distance, but at various points in a semi-circle in front of the opening, at different times. Table I shows the variations in the distance at which the first definite trip was made by each one of the different individuals experimented with, and also the percentage of straight trips made by each individual toward the stone, at the recorded distance, in 10 successive trials.

TABLE I

INDIVIDUAL VARIATIONS AMONG H. INTERPUNCTATA IN REACTIONS TO OBJECTS IN AN EVENLY ILLUMINATED ENVIRONMENT

Specimen	Distance in inches	Percentage of straight trips
1	11	70
2	9.5	90
3	9	90
4	8.5	100
5	7	80
6	7	70
7	6.5	100
8	7	80
9	6	90
10	6	80
11	6	80
12	6	70
13	5.5	100
14	5.5	80
15	5	90
16	5	70
17	4	100
18	4	80
19	3.5	100
20	3	70

In another experiment on variations the same apparatus was used, but the source of light was a 16 candle-power incandescent lamp attached to one end of the basin. In order to reach the stone the nymphs were obliged to swim directly toward the light.[1]

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[1] Wodsedalek, J. E. Phototactic reactions and their reversal in the May-fly nymphs *H. interpunctata* (Say). Biological Bulletin, 1911. vol. XXI., pp. 265–272.

Normally the nymph is decidedly negative in its phototactic response. Fifteen specimens were used, one after another, beginning with the stone one inch away from the opening of the small glass tunnel, on the side toward the light, and then increasing the distance until all of the nymphs reacted negatively.

Here again, we have considerable variation, as is shown in table II. For example, all of the 15 specimens went toward the stone, against the light, when it was between one and two inches away from the opening of the tunnel, and when it was between three and four inches away only about half of them went toward it, while, when the stone was placed six inches away, all of the specimens went in the opposite direction.

The uniformity manifested by the nymphs in their negative response to light when no objects are present, and the obvious variations evinced in their reactions to objects in an evenly lighted environment and also in their reactions to objects against the rays of light, seem to suggest that the specimens going the greatest distance toward the objects have learned to do so through experience in their natural environment.

TABLE II

VARIATIONS AMONG NYMPHS IN THEIR RESPONSE TO OBJECTS AGAINST THE RAYS OF LIGHT

Distance	Toward stone, against light	Away from the light
1 inch	15 trips	0 trips
1.5 "	15 "	0 "
2 "	14 "	1 "
2.5 "	13 "	2 "
3 "	11 "	4 "
3.5 "	9 "	6 "
4 "	3 "	12 "
4.5 "	1 "	14 "
5 "	1 "	14 "
5.5 "	1 "	14 "
6 "	0 "	15 "
6.5 "	0 "	15 "

In order to ascertain whether the reactions to objects are modified by experience, three of the nymphs having similar records in going toward a stone in an evenly lighted environment were taken and with each 21 daily experiments were performed. At the beginning of each set of trials the stone was placed at the greatest distance at which the nymphs went toward it on the preceding day. Usually, the stone had to be brought somewhat closer than this before the nymph made its first trip toward it. Then the stone was taken farther away after each successful trip, until a distance was reached when the nymph seemed to pay no attention to the object. This necessarily had to occur during each set of trials in order to ascertain the greatest distance at which the nymphs would go to the stone. An over-rating of the distance necessitated the bringing back of the stone to a place where another successful trip was made. The distance made each day on the twelfth successful trip was recorded. The results of this test of the learning ability of three individuals are given in table III. The number of inches indicate the distance each nymph would go toward the stone at the end of 12 successful trials. It will be noticed that two of the specimens increased their distance slowly but steadily, while one varied in its daily behavior and even at the end of three weeks apparently had learned nothing.

TABLE III

SHOWING THE LEARNING CAPACITY OF THREE *H. Interpunctata* NYMPHS

Date	Number I	Number II	Number III
1	7 inches	6.5 inches	6.5 inches
2	7 "	7.5 "	8 "
3	7.5 "	7.5 "	8. "
4	8 "	8 "	5.5 "
5	8 "	8 "	7 "
6	7.5 "	8.5 "	8.5 "
7	8 "	8 "	6 "
8	8 "	8.5 "	8 "
9	8.5 "	9 "	7.5 "
10	8.5 "	9 "	5 "
11	8.5 "	9.5 "	8 "
12	9 "	10 "	7.5 "
13	9 "	9.5 "	8 "
14	8.5 "	10 "	8 "
15	9 "	10 "	5 "
16	10 "	11 "	7.5 "
17	9.5 "	10 "	6 "
18	10 "	11 "	8 "
19	10 "	19.5 "	6 "
20	10 "	11 "	7 "

Then 10 specimens that had poor records in going toward a stone against the light were taken and 21 daily experiments were performed with each. The apparatus of the foregoing experiments was used, except that the 16 candle-power incandescent lamp was again introduced at one end of the basin and the specimens, in order to swim toward the stone, had to go directly toward the light. The method of procedure was practically the same as that of the previous investigations. The results were surprising, for most of the specimens gradually inhibited their normal negative phototaxis and proportionately reinforced their positive reaction to the stone. However, the individuals varied considerably. Some showed a slow but steady progress for almost three weeks; some were quite docile for a few days, but soon reached a limit; others learned very little; still others would go toward the stone a fair distance at the end of each set of 21 trials, but had to be started at almost the same distance each day. The four different classes of behavior are represented in table IV.

TABLE IV

SHOWING FOUR DIFFERENT CASES OF LEARNING TO SWIM TOWARD OBJECTS AGAINST THE RAYS OF LIGHT

DAY	SPECIMEN I		SPECIMEN II		SPECIMEN III		SPECIMEN IV	
	First Trip	Last Trip	First Trip	Last Trip	First Trip	Last Trip	First Trip	Last Trip
1.....	1.5 in.	3 in.	1.5 in.	4 in.	1 in.	2 in.	1 in.	4 in.
2.....	2 “	3 “	2.5 “	5.5 “	1 “	1.7 “	1 “	4.5 “
3.....	1.7 “	3.5 “	2.5 “	6 “	1 “	2.5 “	1 “	5.5 “
4.....	2 “	4 “	3 “	6 “	1.2 “	3 “	1.2 “	6.5 “
5.....	2.5 “	5 “	3.5 “	6.5 “	1.5 “	3 “	2 “	7 “
6.....	2.5 “	4.2 “	3 “	7 “	1.2 “	2.5 “	1.5 “	7 “
7.....	2.7 “	5 “	4 “	7 “	1 “	3 “	1 “	6.5 “
8.....	3 “	5 “	4 “	7.7 “	1 “	3.5 “	1.2 “	7.5 “
9.....	3 “	5.5 “	3.5 “	8 “	1.5 “	2.5 “	1.7 “	8 “
10.....	3 “	5.7 “	4 “	7.2 “	1.5 “	2.7 “	2.5 “	7.7 “
11.....	2.7 “	6 “	3.7 “	8 “	2 “	2.5 “	1.5 “	7 “
12.....	3.7 “	6 “	4 “	8 “	2 “	3 “	1 “	6.5 “
13.....	3.2 “	6 “	4.5 “	8.2 “	2 “	2.7 “	3.7 “	8 “
14.....	3 “	6.2 “	5 “	8 “	1.7 “	3.5 “	2 “	7.2 “
15.....	3.5 “	6.5 “	4.5 “	8 “	1.7 “	3.2 “	1 “	6 “
16.....	3.5 “	6.5 “	4. “	8 “	2 “	3 “	3 “	8.5 “
17.....	4 “	6.5 “	5.2 “	8.5 “	2.5 “	3 “	2.5 “	7.7 “
18.....	3.5 “	7 “	5.5 “	8 “	2.7 “	3.7 “	1.7 “	8 “
19.....	3.7 “	8 “	4 “	8 “	1.7 “	3.5 “	1 “	7.7 “
20.....	4 “	7.5 “	5.5 “	8.5 “	2 “	2.5 “	2.5 “	8.5 “
21.....	4 “	8 “	5.7 “	8 “	2 “	3.5 “	1.7 “	7.5 “

Here again, at the beginning of each set of trials the stone was placed at the greatest distance at which the specimen went toward it on the preceding day, and then if necessary, it was brought closer until the nymph made a straight trip toward it, after which the distance was again gradually increased. The number of inches in the first column shows the distance at which the nymph made its first trip toward the stone each day, and that in the second column indicates the distance at which the trip was made at the end of 15 successful trials.

The experiments demonstrate the learning capacity of *H. interpunctata.* Not only did the insect show a tendency to learn in an environment free from disturbing factors, but, as can be seen from the results of the last experiments it learned to do greater and greater distances toward a stone against the rays of light. This is a fact of considerable interest, since these nymphs have a decided negative phototaxis. But, on the other hand they are very positive in their thigmotactic response, and the results seem to indicate beyond doubt that the satisfaction derived through attachment to the stone counteracted whatever reluctance the nymph may have experienced in going against the light.

FEAR REACTIONS

For this set of experiments I first took two large dishes and placed six vigorous specimens in each. Those in one dish were disturbed several times each day, while those in the other were left unmolested. Although the insects always show a tendency to gather into groups when placed in a dish of water, the tendency is greatly diminished in a few days. Such was the case in the undisturbed group. In the group undergoing disturbance this tendency was greatly augmented, apparently through fear. To overcome the grouping propensity the different individuals were put in separate dishes with particles of food too small to enable the insects to attach themselves, and to further obviate the discomfort occasioned through the lack of proper thigmotactic stimuli, the smooth glass bottoms of the dishes were covered with sand.

The room for this research was free from disturbance, and before investigations for the procuring of detailed data were attempted careful observations were made on the behavior of a set of nymphs with a view to detecting and overcoming any undesirable features of the environment. Then, six specimens in separate dishes were placed at one end of the room and subjected to four daily disturbances. In another part of the room were three individuals undergoing one disturbance each day; and some distance away were three more, disturbed but once in three days. In separate dishes scattered among these were six other individuals undergoing no disturbance whatever. Careful observations were made and detailed records of the behavior of all the specimens were kept.

Tables V and VI suffice briefly to show the results obtained with two of the specimens. Their behavior was characteristic of more than half of the 18 nymphs observed in this manner. The letters A, B, C, and D, designate the behavior displayed on the first, second, third, and fourth daily observations respectively. Each one of the three columns is intended for a particular form of behavior displayed by the nymphs, and the letters indicating the behavior manifested during the four daily observations are placed in the columns accordingly. Omission of a letter means that the nymph was not easily disturbed on that occasion. In the first column are recorded the cases of indications of fear only when the specimen was slightly disturbed with a dissecting needle. In column II are given the cases of signs of agitation when a hand was passed back and forth above the dish, and in the last column are indicated the signs of fear displayed by the specimen in the way of swimming about in an excited manner when I appeared before the enclosure. For example, on March 31, on the first observation, which was in the morning, specimen number one showed signs of fear only when the water near it was disturbed with a dissecting needle, and hence (A) was placed in the first column. On the second observation, which was at noon, the nymph began to swim about in an agitated manner when my hand was moved back and forth over the dish, thereby making a place for (B) in column two. On the third observation, which was about six o'clock in the afternoon, the insect displayed indications of fear when I appeared before the enclosure, and so (C) naturally fell in column three. On the last observation on that day, which was late at night, the nymph again showed signs of fear when a hand was moved back and forth over the dish, which caused (D) also to be in the second column.

A glance at either table V or VI at once suggests a curve representing the obvious intensification of the expression of fear. The letters indicative of signs of fear first appear in great numbers in the first column and later gradually make their appearance in columns two and three which represent the more obvious signs of agitation. All of the specimens, however, did not behave in this manner. Some, from the very beginning, would feign death when disturbed, while others reacted very favorably for several weeks and then, on account of their death-feigning propensity, which became more and more pronounced, little could be done with them.

TABLE V

Fear Reactions in *H. Interpunctata*, When Disturbed Four Times Each Day
Specimen I

Date	Indications of fear only when specimen was slightly disturbed with dissecting needle	Manifest signs of agitation when hand was passed back and forth above the dish	Signs of fear displayed in the way of swimming about in an excited manner when I appeared before the enclosure
March 20	C		
21	A C D		
22	B D		
23	A B C D		
24	A C D	B	
25	B D	A	
26	B C	A D	
27	B D	A	
28	A D	B C	
29	A B	C D	
30	B C	D	
31	A	B D	C
April 1	D	A C	B
2	B	A	C D
3	C	D	B
4		B C	A D
5	B		A C D
6		A D	B C
7		C	A B D
8		D	A B C
9	A	B	C D
10		B	A C D
11		B	A B C D
12		D	A B C

TABLE VI

Fear Reactions in *H. Interpunctata,* When Disturbed Four Times Each Day
Specimen II

Date	Indications of fear only when specimen was slightly disturbed with dissecting needle	Manifest signs of agitation when hand was passed back and forth above the dish	Signs of fear displayed in the way of swimming about in an excited manner when I appeared before the enclosure
March 20	B C		
21	A C		
22	A C D		
23	A B C D		
24	A B C D		
25	A C D		
26	A B D	C	
27	C D	A	B
28	A C D	B	
29	A B C D		
30	A B C D		
31	B C D	D	
April 1	A C D	B	
2	B C D		A
3	A B C D		
4	B D	A C	
5	B C D	A	
6	A B	C D	
7	A	B C D	
8	C	A D	B
9	A D	B C	
10	B	A D	C
11		B C D	A
12		A B C D	
13	B	A	C D
14	C	B D	A
15		A B C D	
16		A C D	B
17	D	B	A C
18	B	A C	D
19			A B C D
20		A B	C D
21		B	A C D
22		A D	B C
23		C	A B D
24	C	A	B D
25		B D	A C
26		D	A B C
27		A	B C D
28	A	C	B D

In table VII are given the results obtained with three of the individuals which were observed and disturbed once each day. In this case the numbers 1, 2, and 3, represent the three specimens, and the position of the numbers in any of the columns, like the position of the letters in the two previous tables, indicates the particular kind of behavior displayed by the specimen on that day. For example, on April 13, specimens one and two had to be slightly disturbed before they manifested signs of fear, while specimen number three on the same day showed signs of fear when I appeared before the dish.

TABLE VII

Fear Reactions in Three Specimens of *H. Interpunctata,* When Disturbed Once Each Day

Date	Indications of fear only when specimen was slightly disturbed with dissecting needle			Manifest signs of agitation when hand was passed back and forth above the dish			Signs of fear displayed in the way of swimming about in an excited manner when I appeared before the enclosure	
1	1	2	3					
2	1	2	3					
3	1	2	3					
4	1	2	3					
5	1		3		2			
6	1	2	3					
7		2	3					
8	1	2						
9	1	2	3					
10	1	2	3					
11		2	3					
12		2	3					
13	1	2						3
14	1	2	3					
15	1	2						
16	1		3					
17	1	2	3					
18		2	3	1				
19	1	2	3					
20		2	3	1				
21	1	2						
22	1	2	3					
23	1	2	3					
24	1	2	3					
25		2	3					
26	1	2	3					
27	1	2				3		
28		2	3					
29		2				3		
30	1		3				2	

These results seem to indicate that the nymphs formed few, if any, associations with pain resulting from a single daily disturbance. For the specimens disturbed once in three days there was even less evidence. Their behavior was almost identical with that of the undisturbed group, of which, during two months, one manifested signs of fear only twice; another three times; and four never stirred when I appeared or moved my hand over the dish. In the forms disturbed several times each day, however, even after making liberal allowance for accidental movements, there remains abundant evidence that the nymphs learned to associate my presence with discomfort.

FORMATION OF ASSOCIATIONS IN FEEDING

Training nymphs to come for food is a tedious task. This is due to many reasons, the most obvious of which appear to be: (1) The fact that in their natural environment they always feed attached to the under side of stones with their dorsal side downward; (2) they are moderate feeders and can go a long time—as long as two months—without food; (3) they are strong in their thigmotactic response, and great care must be exercised in dealing with the specimens in order to avoid fear reactions.

Six active specimens were selected and placed in separate dishes without food, in a compartment of the room employed in the experiments on fear. Daily observations were made as regards the position of the nymphs, and considerable time was spent each day in attempting to induce the different individuals to follow food to the end of the dish nearest to me.

At first a piece of alga was brought near the antennae of the nymphs with a pair of forceps. Within a few days practically all of the individuals ate the offered particle. A number of trials showed that only a small morsel of food was necessary each day to insure the proper response the succeeding day. As the nymphs would cling to the piece of alga with their fore claws I would hold on to the food with the forceps and turn the nymph so that it always faced me. This had to be done with considerable care in order not to dislodge the insect or interfere with its feeding. Then I would pull on the piece of food, endeavoring to induce the nymphs to follow. At first they would not move any great distance, but would plant themselves firmly and, if the pull was continued, the particle of food would either break or the nymphs would make an attempt to attach themselves to the forceps.

Later, I would hold a piece of alga near the head of the nymph and when it made an attempt to secure the food I would withdraw a little, in which case the insect would slowly crawl after it. This was a difficult task, for if the food was too far away the nymph would make no attempt to secure it, and again, when it was brought nearer, the insect would make a quick snap at it before I had time to withdraw it. For several weeks I was not able to entice the nymphs to follow the food any considerable distance before they would have their claws on it. However, when this was done the food was not taken away, but, by means of a gentle pull the insect was brought to the part of the dish nearest to me where it was allowed to feed, to a limited extent, undisturbed.

After experimenting with the insects in this manner daily for about four weeks I noticed that most of the specimens would frequently swim after the food when it was brought near them, and would often swim toward me when they happened to be at the further end of the dish when I made my appearance or moved my hand over them. Not all of the individuals which I experimented with reacted so favorably. Some, on account of their decidedly strong thigmotactic propensity, proved to be entirely intractable; while others absolutely refused to eat, and swam about very much agitated whenever a particle of food was brought near them. However, after two and a half months a large majority of the specimens plainly manifested, by means of swimming toward me or clawing against the side of the dish nearest to me, that my presence meant food to them.

From table VIII, on the feeding reactions of three of the specimens, it will be seen that not only did the insects show a growing tendency to remain in the feeding portion of their field, but that they learned to swim after the food. In column I, opposite the number of the day of the experiment, are indicated the positions of the three nymphs A, B, and C, respectively. The (+) sign indicates that the nymph occupied the end of the dish at which I always made my appearance and where the nymph was allowed to feed; the (—) sign indicates that the specimen was at the opposite end. For example, at the time of the observation on the third day of the experiment, specimen A was at the (+)

end of the dish or the end nearest to me, and specimens B and C were both at the (—) end, or the end farthest away from me.

Columns II, III, and IV show the gradual formation of associations in the three specimens. For instance, in column II are given the names of the specimens which have eaten some offered food, but would not follow it on the day opposite which the names are set; column III represents the cases of the same specimens when they followed the food as it was held near their mouth-parts with a pair of forceps; and in the last column are indicated the names of the same specimens which, when present in the (—) end of the dish would swim to the (+) end for food when I appeared or moved my hand over the dish, and the letters A, B, and C, which represent the three specimens, are placed in any one of the last three columns according to the kind of behavior manifested during the different daily observations. For example, on the fourth day of the experiment letters A, B, and C, occur in the second column which means that on that day all three of the specimens ate an offered particle of food, but would not follow it; nor did specimens B and C which were at the (—) end of the dish, swim to the (+) end when I appeared before them. On the twentieth day specimen A, which was at the (+) end of the dish, ate some food but did not care to follow it; specimen B, which was at the (—) end of the dish followed the food when it was held near it with a pair of forceps and hence B is placed in column III; and specimen C on the same date was also at the (—) end of the dish, but it swam toward the (+) end when I appeared and hence C was placed in column IV which is intended for that type of reaction.

It will be seen from the table that all three of the specimens indulged in food within a few days, but that not until the end of three weeks did all three swim after the food when it was offered to them with a pair of forceps. The most obvious signs of the formation of associations, recorded in the last column, did not appear until even later. The number of cases showing that form of behavior are noticeably less than those in the preceding columns, but it must be remembered that during the last days of the experiment the insects occupied the (+) end of their compartment the greater part of the time. Very frequently when the nymphs were at the (+) end at the time of my presence, the ends of the dish would be reversed, causing the specimen to be at the end farther away from me. This action was scarcely complete when the watchful nymphs would again be facing me and immediately proceeding on a rush to regain their former relative position. Such cases, however, are not recorded in the table.

TABLE VIII

Showing Gradual Formation of Associations in Three Specimens of *H. Interpunctata* in Their Feeding Reactions

Date	Column I						Column II			Column III			Column IV		
	Position of the nymphs in the dish. (+) indicates the end of the dish at which I always made my appearance and where the nymphs were allowed to feed; (—) indicates that the nymph was at the opposite end						Indications of the cases in which the nymphs have eaten an offered particle of food, but would not follow it			Record of the cases when the nymphs would follow a piece of food when it was held near their mouth parts			Record of the cases in which when the specimen was present at the (—) end of the dish it would swim to the (+) end when I appeared or moved a hand over it		
	Specimens														
	A		B		C										
1		—	+			—			C						
2		—		—	+			B							
3	+			—		—	A								
4	+			—		—	A	B	C						
5		—	+		+		A					C			
6		—	+		+		A								
7	+			—		—		B							C
8	+		+			—	A	B							
9		—	+		+							C			
10	+			—		—	A								
11		—		—		—	A				B				
12	+		+			—									
13	+		+		+		A	B	C						
14	+			—		—	A	B				C			
15		—		—		—	A								C
16		—	+		+										
17	+			—	+		A	B				C			
18		—		—		—									
19		—	+		+						B	C			
20	+			—		—	A				B				C
21	+			—	+		A								
22		—	+		+				C	A	B				
23		—		—		—	A							B	C
24	+		+		+		A				B	C			
25		—	+		+			B		A					
26		—	+			—				A	B	C			
27	+			—		—				A	B				C
28		—	+		+					A	B				
29	+			—		—			C				A		
30		—	+		+		A				B				

TABLE VIII—*Continued*

Date	Column I						Column II	Column III	Column IV
	Position of the nymphs in the dish. (+) indicates the end of the dish at which I always made my appearance and where the nymphs were allowed to feed; (—) indicates that the nymph was at the opposite end						Indications of the cases in which the nymphs have eaten an offered particle of food, but would not follow it	Record of the cases when the nymphs would follow a piece of food when it was held near their mouth parts	Record of the cases in which when the specimen was present at the (—) end of the dish it would swim to the (+) end when I appeared or moved a hand over it
	Specimens								
	A		B		C				
31......		—	+			—		B C	A
32......		—		—	+			A C	B
33......	+		+		+			B	
34......	+			—		—			C
35......	+			—	+		C	A	
36......		—		—	+			C	B
37......	+			—	+			A B C	
38......	+		+			—		B C	
39......		—	+		+			C	A
40......	+			—	+			A C	B
41......	+			—		—		A B	C
42......	+			—		—			C
43......	+		+		+		A		B
44......		—	+		+		C	B	A
45......		—	+		+			B C	A
46......	+			—	+			A C	B
47......	+		+			—	B	A C	
48......		—	+		+			A C	
49......	+		+		+			B	A
50......	+			—		—			B C
51......	+		+		+			C	
52......	+			—	+			C	
53......	+		+		+		C	A	
54......	+		+		+			B C	
55......	+		+		+			B	
56......		—	+		+		B	A	
57......	+		+		+			C	A
58......	+			—		—		C	B
59......		—	+		+			B	A
60......	+		+		+		A	C	
61......	+		+		+			A	B
62......	+			—	+			B C	A
63......		—	+		+				A C
64......		—	+			—		A	B
65......	+			—	+			A C	
66......		—	+		+			B	
67......	+		+		+			C	B
68......	+			—	+			A	
69......	+								
70......	+	—							A
71......	+	—							
72......	+								
Average.	43	29	40	28	44	24			

Should a line be drawn through the parts of the table where the letters appear most abundantly we should have a gradual curve representing the reinforcement of the reactions to a given stimulus as a result of the formation of associations. The behavior of the three nymphs represented in the foregoing table is characteristic of many other nymphs experimented with. To check these results, daily observations were made in regard to the position and behavior of another set of individuals which had a food supply scattered in small particles at the bottoms of their dishes. Their records show that they exercised no choice between the two ends of the dish, and that they never swam toward me as did those in the training experiments. The trained nymphs no doubt formed an association.

Not infrequently during the work with *H. interpunctata* nymphs did I observe specimens which behaved in an uncommon manner. The most interesting individual which attracted my attention was in the midst of a large number of newly collected specimens in a dish of water. Its peculiar conduct led me to observe it carefully, when I noticed that it skipped about among its fellows, lashing its setae and occasionally making a pass at one of the other nymphs with its front limb like a playful kitten.

It was placed in a separate dish and taken to my room where it was observed and trained daily. After a few days I noticed that its tendency to remain on the upper surface of the stone, whenever the stone was inverted, became more and more pronounced. The nymph was brought to the upper surface in that manner several times each day and on every occasion it was offered a particle of alga. So long as it was treated gently it would remain in that position for a considerable time, but, the moment it was dealt with roughly it would conceal itself under the stone. Great care was taken not to frighten the insect, and within a few weeks it would remain on the upper surface of the rock for hours at a time facing me. Whenever I noticed that the nymph had gone under I would turn the rock over. In about two weeks more, it had almost completely inhibited its shyness and would follow a particle of food to any part of the stone. Then I removed the much coveted stone and placed in the dish a stone bearing a finger-like projection about three inches long. The stone was so submerged that the extreme point of the process projected about half an inch above the surface of the water, pointing toward me. The insect at this stage would readily follow a piece of food to the projection, which became its regular feeding place. At the end of about two months the insect spent practically all of its time, during my presence, perched up near the point of the projection with its head just below the surface of the water. The time and clearness of the day seemed to play no important part on its behavior. Even at night when the electric light was directly over the table on which the insect was located, it would not desert its favorite resting place. Almost invariably, when I had left the room the nymph would soon retire to the under side of the stone. All that was necessary, at this time, to bring the specimen up when it had disappeared from sight was to slightly jar the dish or the table on which the dish was located, and the insect would quickly come up to the upper side of the rock and make directly for its feeding place. Later, very frequently as I stepped into the room I caught the insect in the act of coming out from its hiding-place and halting at the end of the projection ready to receive its usual reward.

Sometimes, when I had been gone from the room all day and did not feed the nymph shortly after my appearance, but simply moved my hand over it, the insect would slowly crawl up on the point of the rock extending out of the water. However, it usually exposed only its head and thorax to the air and apparently exercised considerable care not to expose the abdomen, which bears the tracheal gills. Although I anticipated extended experiments with this entertaining individual, all was brought to a close by its metamorphosis. Nothing more could be done with it in the adult stage, as the Ephemeridae never take food after they emerge, and live but a few days at most. Here again, we have obvious signs of the formation of associations.

Sondheim[1] accidentally made some observations and later performed some experiments with a dragon-fly larva, *Aeschna grandis L.*, and obtained practically similar results during a much shorter time and with far less effort. This is probably due to the fact that the natural habits of *A. grandis* are much different from those of *H. interpunctata.* However, she obtained such results with only a single specimen and although attempts were made to investigate the learning capacity of another larva of the same family, she was unable to get any further evidence of the formation of associations. " Seit einigen Wochen befindet sich wieder eine Libellenlarve in meinem Aquarium, doch habe ich bei ihr noch nicht viel Erfolg mit meinen Fütterungsversuchen gehabt."

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[1] Sondheim, Maria. Wahrnehmungsvermögen einer Libellenlarve. Biologisches Centralblatt, Bd. 21, S. 317-319. 1901.

CONCLUSION

In conclusion it might be said that we have three types of experiments with large numbers of *H. interpunctata* nymphs which clearly show the power of formation of associations by three distinct processes. In case of the investigations on the reactions to objects it was found that the insect gradually increased the distance at which it responded positively to objects in an evenly lighted environment. In another set of experiments it gradually inhibited its usual negative response to light and proportionately reinforced its reaction to an object against the rays of light. It is also important to note the fact that this inhibition in phototactic response was only temporary; it occurred only when the object was present, for whenever the object was removed the nymph would manifest its usual dislike for the bright light. In case of the experimental work on the manifestations of fear through previous experience we have results which can hardly be interpreted in any other way except as a clear example of the associations of my movements with pain, for why should the disturbed specimens show such obvious signs of agitation when the undisturbed group evinced no indications of fear under otherwise practically identical conditions. Lastly, we have results which seem to indicate quite conclusively that the insects associated my presence with food. These results, again, become more convincing when compared with the unvarying individual records of the group not so trained. The foregoing conclusions are not based on the results tabulated in this paper alone, but on the results of a large number of similar experiments performed with many large sets of specimens and continued for two years during the various seasons.

My thanks are due to Professor S. J. Holmes for his kind suggestions and criticisms in preparing this paper.

THE NORMAL ACTIVITY OF THE ALBINO RAT FROM BIRTH TO NATURAL DEATH, ITS RATE OF GROWTH AND THE DURATION OF LIFE

JAMES ROLLIN SLONAKER

From the Physiological Laboratory of Stanford University

Fourteen figures

INTRODUCTION

The purpose of this experiment was to ascertain the normal activity of the albino rat from birth to death due to old age, its rate of growth, and the duration of life. From previous experiments [1] it was seen that to reach these results a number of rats of the same age and parentage should be used. To procure such material female rats of the same litter were segregated and mated to the same male. After a number of trials lasting over a year two sister rats, having been mated to the same male, gave birth to an equal number of young just a day apart. It was of great importance to have the young rats as nearly alike as possible. Previous observations have shown that prenatal and postnatal conditions greatly affect the rate of growth and activity.[4] For example, when the conditions of parentage were as nearly alike as possible the young of a litter of three would have a decided advantage over those of a litter of eight. That is, the individuals of the smaller litter were not only a trifle larger at birth but also grew much faster due to the fact that each received more nourishment than was possible in the larger litter. Since the young had to be nourished by the mother until they were old enough to wean it was deemed very important that not only should the mothers be as nearly alike and related as possible, but that each litter should be of the same number and age. With this material in hand conditions were as nearly ideal as it was possible to obtain.

In selecting the young for the experiment an equal number of each sex should be used, but owing to the fact that the external sexual characters are not easily distinguishable at the weaning time it was not possible to secure this ideal condition.

Eight young were selected from the two litters. They were arranged and designated in the following manner: 1 and 2 from litter A; 3 and 4 from litter B; 9 and 10 from A; and 11 and 12 from B. Numbers 1 to 4 inclusive were placed in revolving cages to ascertain their normal activity as manifested by voluntary running. The remaining four (9, 10, 11 and 12) were used for controls and were placed in stationary cages in which rats are usually kept. In every case each rat was in a cage by itself. This was its home during its life from which it was removed only for a time sufficient to weigh the animal and clean its cage. It was later ascertained that in this selection six males and two females had been chosen. Fortunately three males and one female comprised each of these two groups of four. Numbers 1, 2, 4, 9, 10 and 12 were males; 3 and 11 were females.

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[1] Slonaker, J. R. The normal activity of the white rat at different ages. *Jour. Comp. Neurol. and Psychol.*, 1907, vol. 17, pp. 342-359.

The apparatus used for recording the activity has been previously described.[2] In brief it consisted of a large cylindrical cage which revolved on a stationary axle. On the axle was fastened the nest box, the food box and the water pan. The cage revolved only when the rat ran. The number of revolutions were automatically registered and at the same time each revolution was automatically marked on paper kept moving by a continuous roll kymograph. By the first device the exact number of revolutions in a given time or the total number could be readily ascertained for each rat. By the second contrivance the distribution and length of periods of activity and rest during the day, night and lifetime could be consulted and compared at any time. This graphic representation of the activity has been of great assistance as only by this means do the characteristics of the activity due to different ages appear.

Only that phase of the activity of the rat manifested in voluntary running has been considered in this research. It was impossible with this apparatus to record any of the other activities. However, numerous observations of the activities of the rat readily convinces one of the fact that though running is only one phase of activity it goes hand in hand with and is directly proportional to the other activities. That is, if a rat is in general very active at a given age it does a great deal of voluntary running which has an apparent definite ratio to the other activities. For this reason this one phase of the normal daily activity has been taken as an indicator of all the activities of an individual.

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[2] Slonaker, J. R. Description of an apparatus for recording the activity of small mammals. *The Anat. Record,* June, 1908, vol. 2, pp. 116-122.

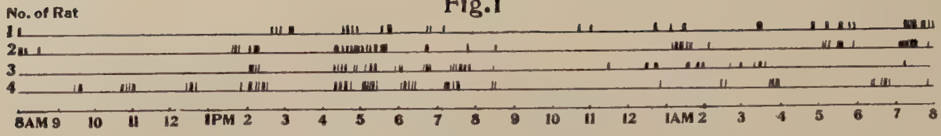

Fig.1

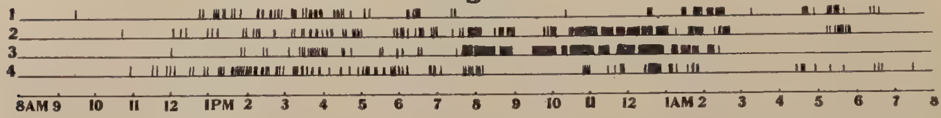

Fig.2

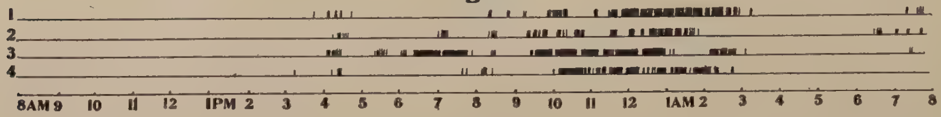

Fig.3

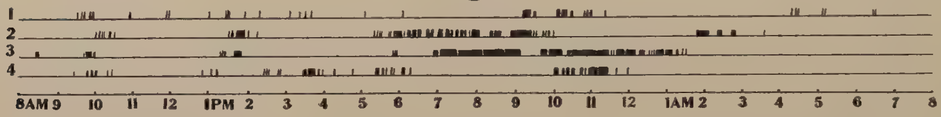

Fig.4

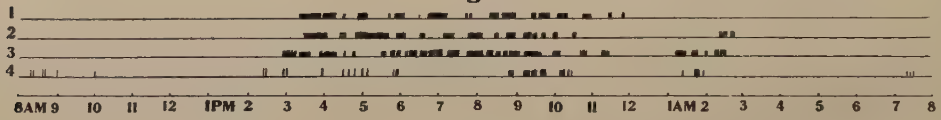

Fig.5

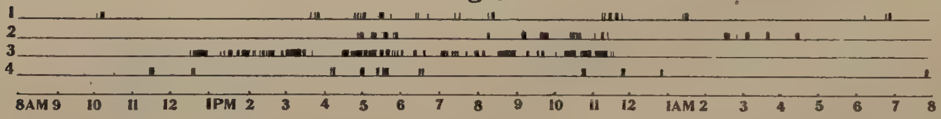

Fig.6

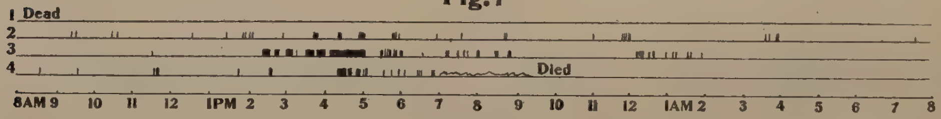

Fig.7

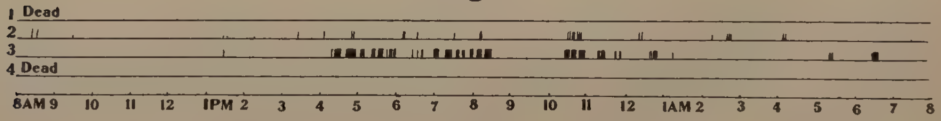

Fig.8

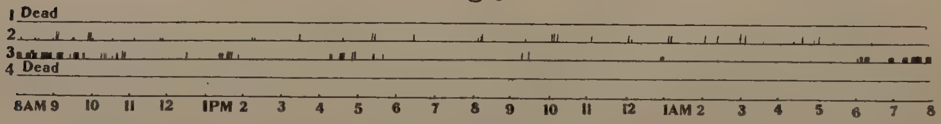

Fig.9

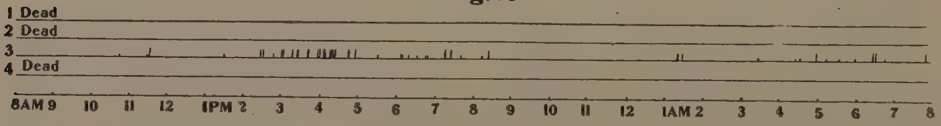

Fig.10

In connection with their activity it was very easy to determine the rate of growth and final decline due to old age. Careful weighings were taken at sufficient intervals to indicate this.

DISTRIBUTION OF THE DAILY ACTIVITY

The young were taken from their mothers when they were 28 days old. They were carefully weighed and placed in their individual cages as has already been noted. Hereafter they will be designated by the numeral given each.

When first introduced into its cage each rat showed a marked degree of curiosity. It examined every corner and object within the inclosure, using mainly the sense of smell assisted by the sense of touch and to a still less degree that of sight. After about an hour of such investigation most of those in the revolving cages had found their way to the nest boxes in which they remained for a time. The graphic record of their activity (Fig. 1) shows that their periods of activity and rest were numerous. The activity would consist of a few turns of the cage then rest soon to be followed by another short run. In only a few cases did an individual keep up the activity longer than a few minutes at a time. At this age the periods of activity were not confined to any special part of the day, but were rather uniformly distributed throughout the 24 hours. Coupled with this activity manifested in running was that accompanying investigation by the animal as already noted. After a few days, however, they became familiar with their surroundings and appeared to be perfectly at home. Their activity then was characterized by their running. At intervals they would frisk and jump about in play, a characteristic of most young animals. As they grew older this playfulness became gradually less and less and was replaced by more uniform and regular running.

By consulting Figs. 1–10, which are graphic records of the

FIGURE 1. Graphic record as recorded by the kymograph of the activity when the rats were 32 days old and 4 days after they had been weaned and placed in the revolving cages.
FIGURE 2. Graphic record of activity at the age of 6 months.
FIGURE 3. Graphic record of activity at the age of 11 months.
FIGURE 4. Graphic record of activity at the age of 16 months.
FIGURE 5. Graphic record of activity at the age of 21 months.
FIGURE 6. Graphic record of activity at the age of 25 months.
FIGURE 7. Graphic record of activity at the age of 26 months.
FIGURE 8. Graphic record of activity at the age of 28 months.
FIGURE 9. Graphic record of activity at the age of 31 months.
FIGURE 10. Graphic record of activity at the age of 34 months.

activity at the ages indicated, one can get a good idea of the nature of their activity. Fig. 1 represents their activity at the age of 32 days, or four days after they had been weaned and placed in the revolving cages. As can be readily seen the periods of continuous running are of very short duration. Also the periods of activity and rest have no definite arrangement with respect to the hours of the day. The longest period of continuous rest is about six hours and the longest period of continuous activity lasts but a few minutes. This result was no doubt due to the fact that at this age the young are accustomed to feeding at frequent intervals. Since the rats could not go from their nests to the food without jumping on to the revolving cage they left their graphic records each time they passed from the nest box. But one must not infer that each graphic record represents a feeding time. Numerous observations proved that they revolved the cages many times without going near their food.

Fig. 2 is the graphic record at the age of six months. This shows some marked changes. Though they still show a more or less restless disposition throughout the 24 hours the main part of their activity is confined to the hours between 7 p. m. and 3 a. m. During these hours they ran almost continuously for periods of 30 or 40 minutes at a time. The records are slightly misleading in this respect. The kymograph paper moved so slowly that intervals of two or three minutes could occur without a break or space showing in the record. A solid block on the record, therefore, does not necessarily mean that a rat has run continuously without a single stop for the time indicated. The longest period of continuous running without a single stop which was observed was between four and five minutes. During this time they would often turn the cage at the rate of a hundred or more revolutions per minute. After a rest of a minute or so they would again run for a number of minutes. The record of activity would thus appear to be continuous so long as the interval of rest was not longer than about two minutes.

The very intermittent and irregular activity seen from 11 a. m. to 7 p. m. is easily explained. They were accustomed to being fed between 3 and 5 p. m. At this age they were more or less restless for an hour or so before feeding. After feeding they carried all they could conveniently into their nest boxes.

On this day they were fed at 3:20 p. m. It is noticeable that at this age they had become much more regular in their habits and, having become thoroughly accustomed to their surroundings, did not manifest the investigating nature which was so prominent when they were younger. The playfulness which was so conspicuous at an early age was less marked.

In Fig. 3 is seen the record of their activity at the age of 11 months. It is now noticed that the activity begins mainly with the feeding time (4 o'clock) and is practically complete at 4 a. m. Activity and rest are thus divided into two almost equal periods of 12 hours each. The period of activity being confined mainly to early twilight and night and that of rest to day time. Playfulness in action was not manifest at this age.

At the age of 16 months very little change is to be noted in the general activity (Fig. 4). A week previous to this record the feeding time was changed to the morning to determine what effect this would have on the distribution of their activity. As is readily seen the usual random running found to generally follow the feeding shifts to the morning, but the great bulk of voluntary running occurs during the period of darkness and is apparently in no way affected by the change in the time of feeding. In other words the albino rat, like the wild Norway rat, is nocturnal in its habits.

Fig. 5 is the record of their activity when they were 21 months old. At this age the rats were almost wholly inactive from 3 a. m. to 3 p. m. Their day was thus divided into two equal periods of 12 hours each. Number 4 is beginning to show the effects of old age as the periods of activity are of relatively short duration and are separated by relatively long periods of rest. Also this rat, though it has still done the greatest amount of running during the night, has been more or less active throughout the entire day. This is especially noticed in the records of all at older ages. In other words, as the rats reach old age their activity resembles more and more that of the very young rat in distribution, but is less in amount.

At the age of 25 months a marked diminution in the amount of running is noticed (Fig. 6). It is now very obvious that the female (No. 3) is much more active than the males (Nos. 1, 2, and 4). The activity of each of the males is very similar and shows the characteristic activity of rats in old age. Their movements were very slow and feeble having lost all the alertness and quickness common to their youth. The record of No. 1 represents its activity just two days prior to death due to old age. During the last day of its life this rat turned its cage 94 revolutions which was a small amount compared with over 6,000 accomplished in the prime of its life.

Fig. 7 represents the activity at the age of 26 months. The two remaining males, Nos. 2 and 4, show the characteristics of old age, while the female No. 3 still shows the activity characteristic of middle life. The record for No. 4 shows the last day's work of this rat which consisted of 48 revolutions. It also shows its final death struggles which began at 7 p. m. and ended soon after 9.

The remaining figures, 8, 9 and 10, show the effect of extreme old age. They represent the ages of 28, 31 and 34 months respectively. Fig. 9 shows the record of No. 2 just two days previous to its death. It is quite similar in its appearance to that of No. 3 in Fig. 10, which is the record of this rat just two days prior to its death at an age of almost 34 months.

From the observations of the records (Figs. 1 to 10) of any one rat, from the first to its death, the following points may be easily seen:

1. The daily activity increases with the advance in age until a certain age is reached, after which there is a gradual reduction till death occurs.

2. Distribution of the activity. In youth it is rather uniformly distributed over the entire 24 hours. With maturity activity becomes concentrated into one period and rest into another. In extreme old age the activity becomes scattered and resembles that of the very young.

3. During the prime of life the albino rat shows almost continuous activity for periods of as much as two hours at a time (Fig. 4, No. 3).

4. The albino rat is nocturnal in its habits.

5. This female is much more active than any of the males.

THE AMOUNT OF DAILY ACTIVITY

We have just considered the character of the activity of the rat at different ages in regard to its distribution during the entire day. Let us now consider the actual amount of running activity exhibited at the different ages. Owing to the device which recorded the number of revolutions it is very easy to estimate the distance run each day during the life time. Since the change is so gradual and a computation of each day would be so voluminous I have considered computations made once each month sufficient to represent correctly the change in the

TABLE I

Average Daily Revolutions at Ages Indicated

Age in Months	Rat No. 1 (Male)	Rat No. 2 (Male)	Rat No. 3 (Female)	Rat No. 4 (Male)
1	348	1002	620	448
2	1200	1124	2118	1336
3	790	886	1956	1832
4	5028	5850	5782	6620
5	1206	3930	7280	834
6	540	1644	8482	540
7	1307	3144	10185	3574
8	2084	3274	9518	4276
9	6002	7574	8930	2836
10	2616	4398	8260	2882
11	3620	2096	8640	2310
12	2186	4258	8902	2616
13	3860	7066	11044	3084
14	3860	6374	10992	3004
15	1428	4768	8198	2556
16	1006	2642	13002	1364
17	2684	4776	5982	1998
18	744	2364	9732	1512
19	996	2476	8312	808
20	806	2056	9658	720
21	690	1520	3210	482
22	336	1810	5468	290
23	1696	1680	3188	456
24	380	1352	3100	220
25	94*	1466	4612	196
26	....	188	2538	48*
27	....	160	1968	....
28	....	180	5171	....
29	....	72	2424	....
30	....	56	2832	....
31	....	28*	1706	....
32	....	....	2312	....
33	....	....	488	....
34	....	....	435	....
35	....	....	60*	....

* The number of revolutions made during the 24 hours previous to the death of the animal.

amount of running activity during the lifetime. In order that the figures representing the activity at a given age may not represent a single day's run, but an average day's run at that age the following scheme was used. The number of revolutions for the five days preceding and the five days succeeding the day representing the age desired were taken and from these an average day's run was estimated. This eliminates the possible effect of food, temperature, or other conditions which might cause a sudden slump or increase in the activity of a given day.

Table I represents such averages and shows the average number of revolutions made each day by each rat at the ages indicated. Consulting this table it is readily seen that in each case there is a rapid increase in average daily running. But instead of its being a uniform increase it was rhythmic in character. There was a rapid increase in the amount of activity for a month or so after which there was a decrease. This was followed again by another increase and decrease. The rhythmic effect is best shown in Fig. 11. These curves show the average daily running for each rat at the ages indicated. In other words it is the data of Table I put in the form of curves. The difference in the average daily activity of the males and the females is very noticeable. It is also interesting to note that the rhythmic increase and decrease of activity of each of the males accords very closely as to time, while that of the female does not correspond so closely. So far I am not sure of the causes which underlie this rhythmic variation. These changes correspond more or less to the fluctuations in the weight of the rats as shown in Fig. 13. The causes for the changes in weight will be discussed later under the topic of growth. I will, however, state that following an increase in the amount of protein food given there was an increase in weight accompanied generally by a greater or less increase in activity. But as the results are not always constant there must be something else which influences and causes these rhythmic fluctuations. If the changes in activity of the female corresponded closely to those of the males or as closely as the males do among themselves I would consider they might be due to the periods of heat. At such times there is a tendency in both sexes when near each other to excessive running. The fact that No. 2 and No. 4 were situated one on each side of No. 3 and that these two males did more running

Fig. 11

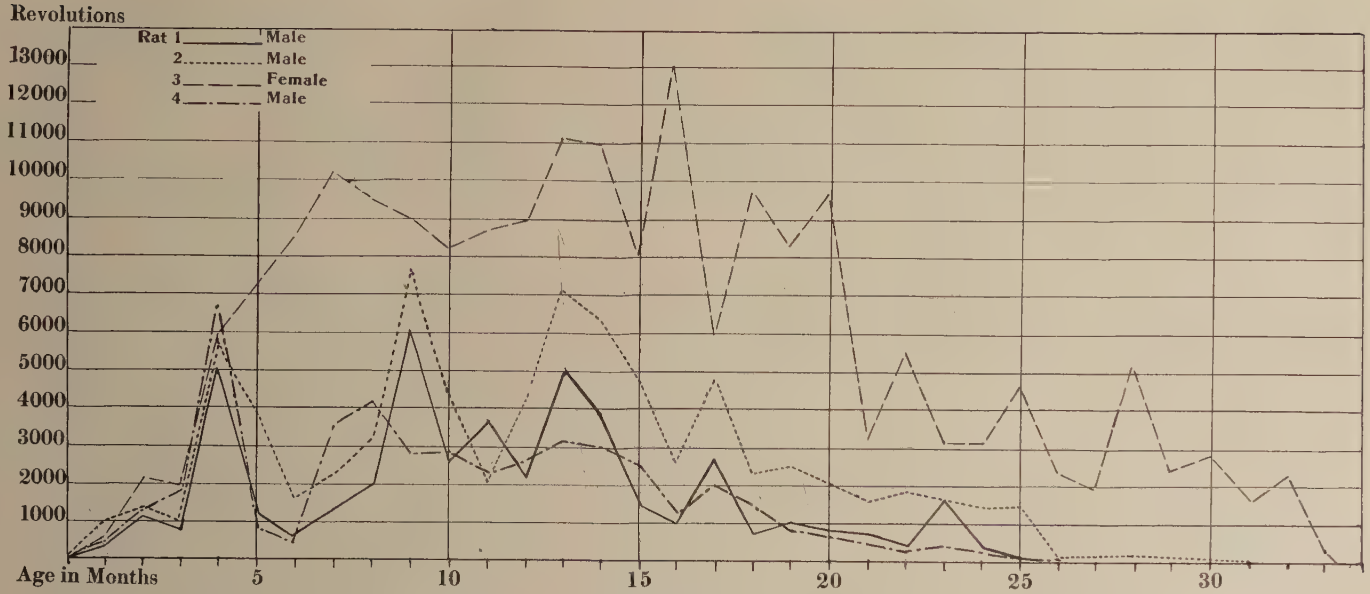

FIGURE 11. Curves representing the average daily activity of each rat at the ages indicated.

than No. 1, which was farthest away, would seem to indicate that this supposed condition may have had its influence. Though this supposition may be true, owing to the differences in the curves of the two sexes, one is not justified in placing very much credence in it. Other changes in their environment no doubt are responsible to some extent for these fluctuations. This will be discussed in more detail later.

By comparing the figures in Table I and the curves in Fig. 11 a marked difference is observed in the average daily activity of the two sexes. For the first four months there is not much difference, but after this age the female excels the males to a great extent, and is never equaled by them again. The greatest average daily run as shown in this table was accomplished by the female and consisted of 13002 revolutions, or a distance of 11.2 miles. This same rat has a record of 14.2 miles during 24 consecutive hours. The greatest average daily run of any of the males was 7574 revolutions. which was equivalent to 6.6 miles. The greatest average run for the four rats was at the age of nine months. At the age of four months a uniform and very marked rise in the curves is noticed, but as each rat with the exception of No. 4 surpasses this amount of activity at a later age this cannot be considered the age of greatest activity. It is true, however, that the average for the males alone is greater at this age than at any later time but it exceeds by only a few revolutions. Hypothetical curves representing the mean between the two extremes of activity for males and females would show the greatest amount of work for the males at about the tenth month and for the female at about the age of 12½ months. Owing to the fact that there was but one female too much dependence cannot be placed on this result since it was not an average. It is interesting to note, however, that the ratio of the age of greatest activity (10 months) of the males to the average age of their death (27 months) is 1:2.7 which is practically the same as that for the female (12.5 months: 33.8 months) 1:2.7+. If this ratio can be depended upon, a normal white rat would voluntarily do the greatest amount of daily work at an age a little older than one-third that of its whole normal life. It would be exceedingly interesting to know if this ratio would apply to other animals.

TOTAL AMOUNT OF ACTIVITY DURING LIFE

Table II represents the total amount of activity of each rat at the different ages as indicated by the number of revolutions. In order that this data may be more comprehensible not only the number of revolutions is given but also the equivalent distance in miles. This same data is represented in the form

TABLE II

Total Number of Revolutions and Distance Run at the Ages Indicated

Age in Months	Rat No. 1 (Male)		Rat No. 2 (Male)		Rat No. 3 (Female)		Rat No. 4 (Male)	
	Miles Run	Number Revolutions	Miles Run	Number Revolutions	Miles Run	Number Revolutions	Miles Run	Number Revolutions
1	1	1200	2.6	3050	1.1	1300	1.7	2060
2	16	18850	22	26140	19	23010	19.6	23390
3	68	79750	77	91130	95	111320	100	118150
4	121	148460	160	189620	170	201730	210	248780
5	211	248990	273	322420	336	406780	346	409250
6	278	329900	373	438020	572	672070	495	508500
7	341	403070	434	523320	882	1041330	550	656470
8	414	487130	551	650490	1181	1388260	658	777640
9	487	576360	663	786660	1435	1678890	740	870400
10	612	722880	832	982210	1710	2028190	810	952860
11	691	817000	915	1082000	1980	2332260	876	1039650
12	749	883120	1023	1215190	2230	2647640	945	1104240
13	812	961360	1155	1378680	2490	2938160	1036	1218620
14	900	1068300	1318	1548570	2780	3286540	1115	1319100
15	986	1165990	1390	1666150	3020	3559830	1168	1389940
16	1020	1206980	1490	1760900	3230	3820590	1220	1455930
17	1080	1271700	1560	1849340	3460	4091400	1270	1488930
18	1110	1309080	1665	1975140	3650	4318780	1298	1529400
19	1125	1339080	1747	2072520	3890	4599500	1325	1571080
20	1165	1382130	1850	2146720	4125	4867910	1347	1588710
21	1188	1400500	1862	2203380	4280	5076100	1358	1601920
22	1210	1429570	1920	2277120	4475	5290770	1362	1613700
23	1225	1457500	1980	2334160	4620	5462560	1380	1624420
24	1244	1469340	2025	2380260	4720	5573480	1385	1631780
25	1265	1486250	2050	2423250	4810	5679360	1389	1639060
26			2078	2447180	4900	5796630	1391	1642100
27			2090	2456190	5000	5909860		
28			2093	2469110	5100	6018140		
29			2095.6	2462520	5180	6118320		
30			2097	2463950	5250	6202570		
31			2097.7	2464770	5300	6259910		
32			2098	2465130	5350	6353920		
33					5430	6414900		
34					5447	6427500		

Fig.12

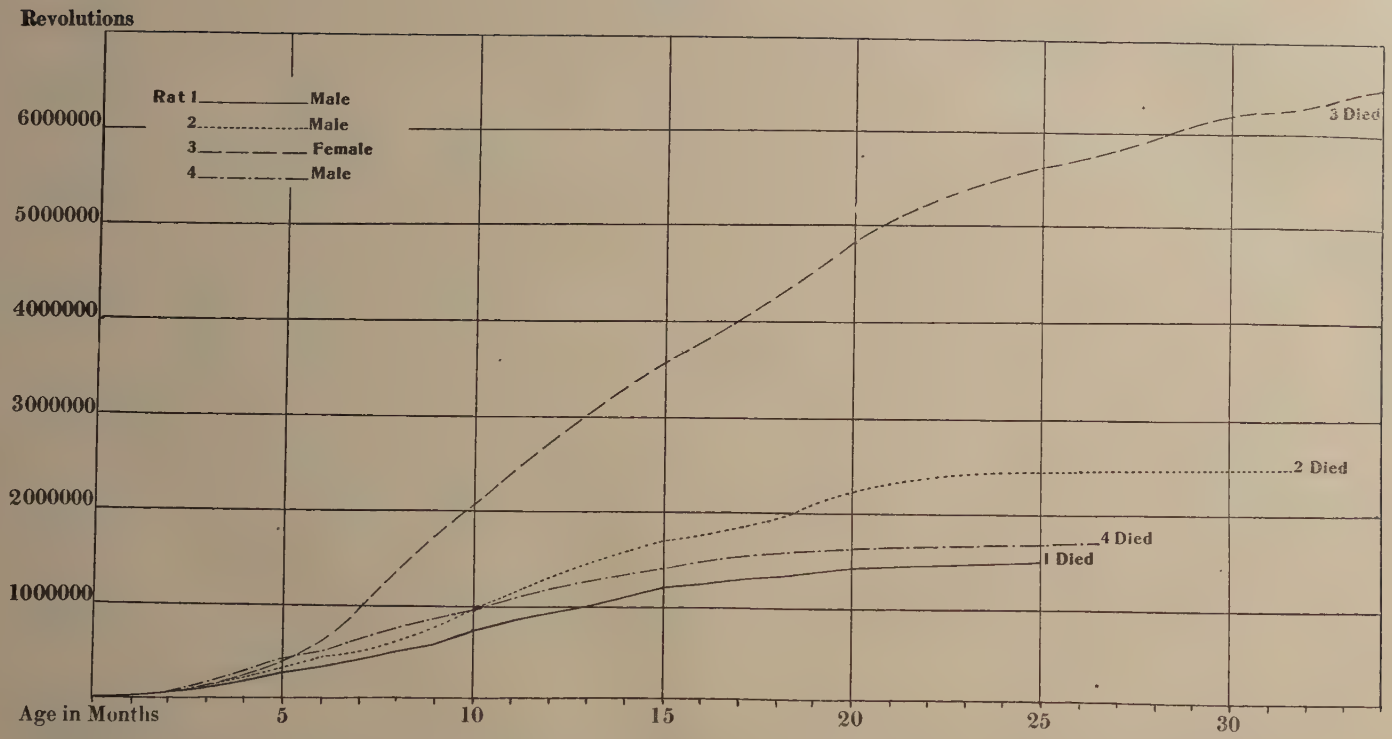

FIGURE 12. Curves representing the total amount of work and the rate it was performed of each rat during its lifetime.

of curves in Fig. 12. The most noticeable thing in this figure is the great difference existing between the males and the female. They all kept fairly close together until the fifth month of age. After this the female, No. 3, rapidly surpassed the males in total amount and ended her life with a total run of 5447 miles. This distance is nearly three and one-half times as great as the average distance run by the males. In other words the ratio of total activity of the male to the female was 1:3.44.

It seems almost incredible that a rat would run 5447 miles during its lifetime. For this rat it was an average run of a little less than 5.5 miles each day. During its very young days and its old age it did not run this distance each day. Throughout the prime of its life, however, it was no uncommon thing for it to run 10 or 12 miles a day. The males averaged less than two miles each day during their lifetime. Since the main bulk of the activity was confined to the 12 hours from 3 p. m. to 3 a. m. we can see that the rate of running for the female averaged almost one-half mile each hour and for the males a little less than one-sixth of a mile per hour of activity during their lifetime.

We have already said that the greatest amount of daily activity was accomplished by the males at the age of 10 months and by the females at the age of 12.5 months. What portion of the total amount of work accomplished during their lifetime had been performed at these ages? Table III shows not only this but also the ages and the percentage equivalence of total

TABLE III

PERCENTAGE OF TOTAL LIFE SPAN REQUIRED TO DO CERTAIN FRACTIONAL PARTS OF THE TOTAL LIFE'S WORK AND THE AGE IN MONTHS AT WHICH THESE AMOUNTS OF WORK ARE COMPLETED.

Fractional part of total amount of life's work		1/8	2/8	3/8	4/8	5/8	6/8	7/8
Males (Average for 3)	Percentage of life equivalent to age	16.1	21.4	32.1	36.4	46.4	53.8	67.9
	Age in months....	4.5	6	9	10.2	13	15	18
Female (Average for 1)	Percentage of life equivalent to age	19.1	26.1	32.3	41	48.8	53.8	72.6
	Age in months....	6.5	8.9	11.1	13.8	16.6	19.9	24.7

lifetime at which certain arbitrary fractional parts of the total amount of work was performed. The males had accomplished one-half of their total activity at the age of 10 months, which represented 36.4 per cent of the whole life time. When the female had performed half of its total activity it had reached the age of 13.8 months or 41 per cent of its lifetime. This was at a trifle later age than when this rat accomplished its greatest amount of daily activity.

This table shows us some very interesting things. It shows that the males turn off their work at an earlier age in life, representing a lower percentage of lifetime than the female. This is true in the case of each of the arbitrary fractional parts of their total work which has been selected. One-half of the total work has been accomplished when but 36.4 per cent of the male and 41 per cent of the female's life has been passed. When seven-eighths of the total work was done they still had about 30 per cent of their lives to live. In other words only one-eighth of their work was still left for them to do during this comparatively long time. This shows a marked contrast in the activity of youth and old age. In the young males for example it required but 16.1 per cent of their lifetime to do one-eighth of their life work, while in old age it required 32.1 per cent of their lifespan to perform the same amount. At this latter percentage of lifespan they had accomplished in their youth three-eighths of the total work.

Since these animals were in no way compelled to work but did it of their own volition we can readily conclude that we might expect a greater amount of work during youth up to middle age than in the latter half of life. I think one is justified in saying also that such animals could be driven to do a much greater amount of work during the first half of their life than the last half. From general observations and these data I believe one is warranted in saying that similar results would be obtained from other animals including man.

THE RATE OF GROWTH AND LENGTH OF LIFE

Owing to the fact that the mothers sometimes destroy their young when they are disturbed no weights were made of the young until they were weaned. Other investigators have studied the growth of other animals from birth. They have come to the general conclusion that the greatest percentage of gain in weight is made soon after birth and this percentage of increase diminishes rapidly during the first month of life.

Minot [3] has found that in the growth of rabbits the average daily gain up to five days of age is 17.6% for the males and 16% for the females. At the age of from 25 to 30 days the gain had dropped for the males to 5.3% and for the females to 6.8%. In the case of the growth of the chicken the average daily increase drops from about 9% on the fifth day to about 5% on the thirtieth day. He found a somewhat similar condition to obtain in the guineapig.[4]

Donaldson [5] in speaking of the growth of man says "* * * from birth to the first year there has been an increase in weight of 240% for the males, and 190% in the females. But this rate diminishes during the succeeding years with astonishing rapidity."

Miller [6] in a paper on the Norway rat has found that the male is 52 mm. long and the female is 49 mm. at birth. The average weight of both sexes at birth was found to be 6.4 grams. There was a gain of from 1/7 to 1/10 in 24 hours. By the seventh day they had doubled their weight; by the eleventh day they had trebled it; by the fifteenth, they had quadrupled it; and by the seventieth day they had reached an average weight of 115 grams, or 18 times their weight at birth. This is somewhat heavier than the average albino rat, but no doubt the same relative increase would occur during the first month. The average weight of the albino rat at the age of 70 days, according to Table IV, is 84 grams.

In order to determine the growth the rats were weighed before feeding at intervals of about two weeks. This was often enough to show the changes in weight during the life time. It was found that the changes in weight were fairly gradual and that weights taken at greater intervals would be sufficient. Accordingly the weights which were made about a month apart were selected in constructing Table IV. Figs. 13 and 14 were

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[3] Minot, C. S. The problem of age, growth and death. 1907, pp. 254 and 258.

[4] Minot, C. S. Senescence and rejuvenation. First paper—On the weight of guinea pigs. *Jour. of Physiol.*, vol. 12, 1891, pp. 98-153.

[5] Donaldson, H. H. The growth of the brain, p. 62.

[6] Miller, Newton. Reproduction in the brown rat. (*Mus. Norwegicus*). Amer. Nat. 1911. vol. 45, pp. 623–635.

TABLE IV

SHOWING RATE OF GROWTH AS INDICATED BY THE INCREASE IN WEIGHT. THE MAXIMUM WEIGHT ATTAINED IS IN BOLD FIGURES. WEIGHTS ARE IN GRAMS.

AGE		EXERCISED RATS IN REVOLVING CAGES				CONTROL RATS IN STATIONARY CAGES			
Mos.	Days	No. 1 Male	No. 2 Male	No. 3 Female	No. 4 Male	No. 9 Male	No. 10 Male	No. 11 Female	No. 12 Male
	30	42	43	37	39	34	45	39	45
2	11	79	89	76	68	84	100	84	92
3	5	107	123	107	99	146	157	124	141
4	5	132	143	123	128	183	200	140	178
5	3	145	165	136	145	214	225	154	205
6	3	170	179	141	169	241	249	165	242
7	4	179	195	152	185	265	262	174	265
8	13	201	219	158	205	282	283	181	292
9	13	206	218	161	222	288	289	180	298
10	11	215	245	163	221	291	301	184	308
11	9	217	248	161	226	296	304	**200**	315
12	13	226	247	159	230	308	322	199	309
13	2	232	265	170	238	**310**	**331**	135*	**319**
14	3	234	259	168	246	291	295		296
15	1	231	254	164	240	291	295		294
16	17	242	**272**	168	252	286	300		298
17	1	249	268	**176**	257	289	298		304
18	4	**252**	270	165	258	302	310		313
19	22	245	269	159	**261**	297	293		310
20	24	240	244	153	249	290	282		291
21	15	245	262	161	250	290	284		290
22	12	244	270	163	254	295	280		294
23	7	235	261	159	242	288	270		292
24	10	235	269	163	248	292	283		294
25	6	214	271	155	233	290	283		284
26	18		259	148	215	278	272		297
27	18		252	154		287	275		294
28	7		256	139		284	278		294
29	7		251	147		293	270		302
30	15		263	157		288	268		300
31	7		264	163		288	263		304
32	5		206	151		279	269		302
32	20			145		271	258		285
33	9			159		264	252		280
33	26			128		259	251		277
34	26					264	249		280
35	9					247	225		268
36	2						242		277
37	10						229		269
37	25						227		259
38	18						226		238
39	6						225		230
40	6						220		225
40	24						210		203
41	11						203		
44	16						185		
45	12						170		

* This rat was killed because of sickness.

constructed from the data in this table and represent the curves of growth of each of the exercised rats and the control rats respectively.

By comparing Figs. 13 and 14 it is readily perceived that the control rats reach a heavier weight and also live longer than those in the revolving cages. This is especially noticeable

Fig.13

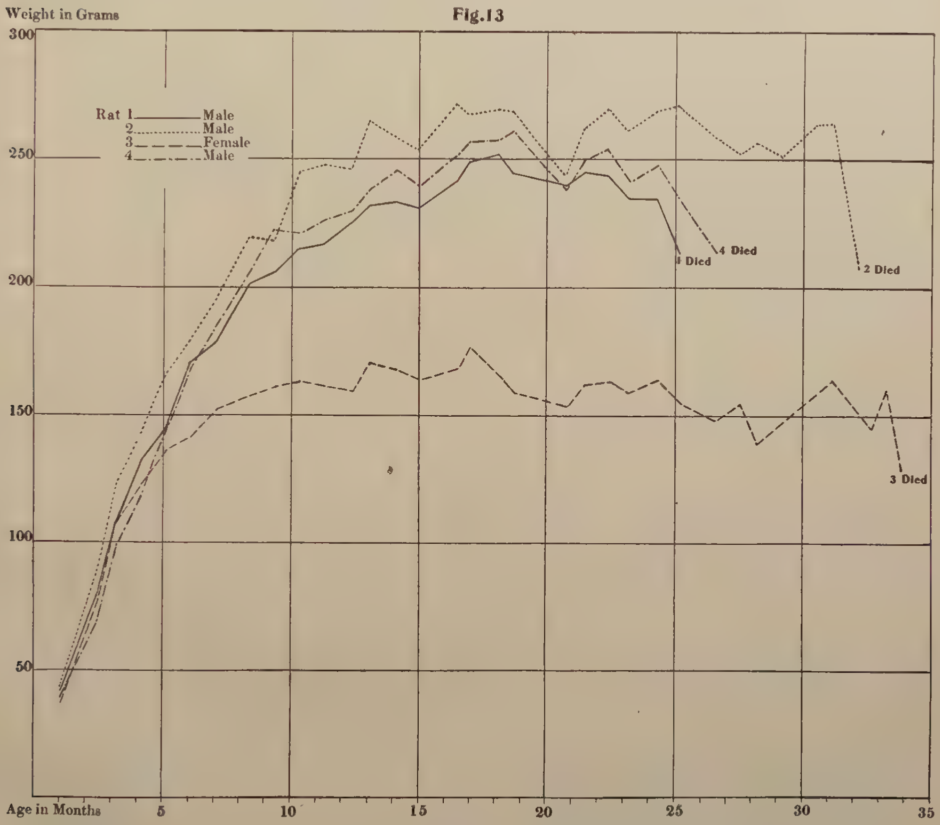

Figure 13. Curves representing the growth and decline of the exercised rats during their lifetime.

when the males are compared. The exercised and control female rats can be compared only during the first 11 months. About this time No. 11 showed signs of illness. At the age of 13 months the malady had developed into a disease common to the white rat. It had been kept in hopes that it would recover, but as it was rapidly declining and there was great danger of the other rats becoming infected this one was killed. They can, however, I think be relied upon to the eleventh month as it seemed perfectly normal in every respect. Whether it would have reached a heavier weight than 200 grams can not be predicted, but judging from the growth of the others I feel convinced that it would have grown to a larger size had it been in normal health.

Fig. 14

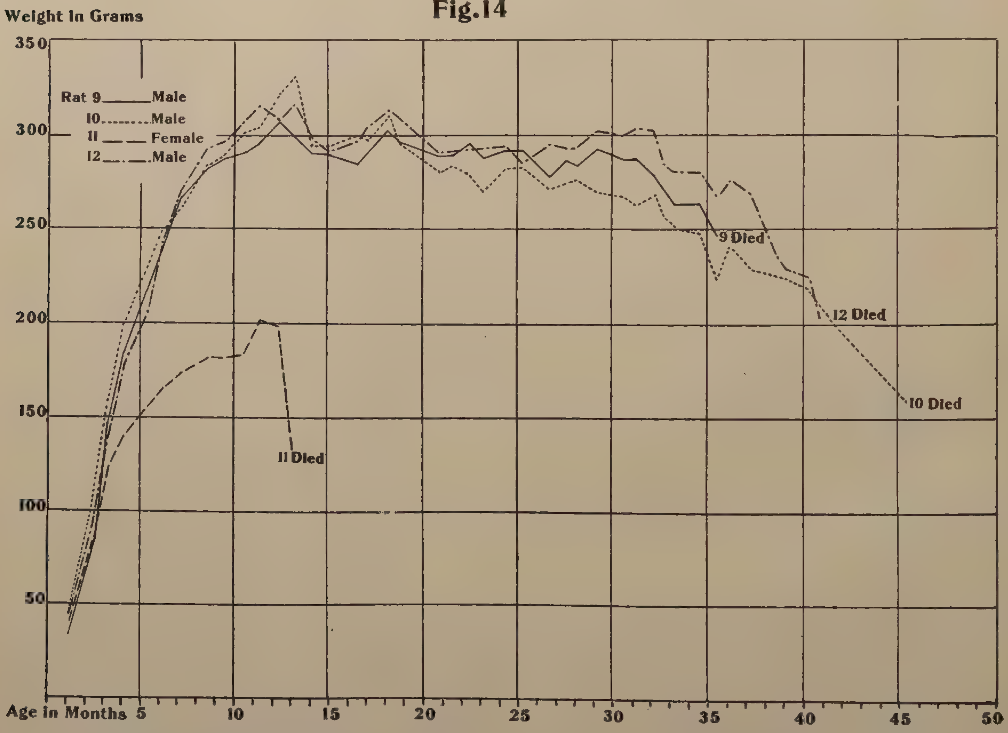

FIGURE 14. Curves representing the growth and decline of the control rats during their lifetime.

The curves representing growth show rhythmic fluctuations somewhat similar to those seen in the curves of daily activity in Fig. 11. These fluctuations in growth compare in a general way with those of daily activity. In some cases they compare directly in time and appearance. Only a few comparisons will be made. At 13 months old there was a general increase in daily activity (Fig. 11), also a general increase in weight

(Figs. 13 and 14), followed in each case by a noticeable decline in activity and weight. This decline was followed by another rise in activity and weight at about the age of 17 months. Again a similar rise though not so marked is noticed at the age of 23 months. These changes are often largely due to changes in food. Previous to and during each of these increases food richer in protein was fed than during the periods of decline. These changes in weight are not, however, always due to changes in food. Many other conditions enter to bring about these results, as they often occur when their diet is as nearly constant as possible. The following example will suffice. A very noticeable depression is seen ending the 21st month. During the two months previous to this date workmen were busy making repairs incident to the earthquake of April 18, 1906. These repairs necessitated a great deal of pounding and confusion in the adjacent room, which was connected by ventilators to the experiment room. Old plastering had to be removed and new put on, which caused a great deal of dust and noise. In this case I think it was the confusion and dust that caused the rapid decline in activity and weight as the diet had been such as to maintain uniformity in these respects.

I attribute the difference in weight between the control and exercised rats to the fact that the control rats did not have a ready means of exercise. They could give but a jump or two before they would be at the end of their run. In other words there was nothing to stimulate exercise. As a result the energy which would have been expended in exercise had favorable conditions been offered was used in growth. The experience of stock raisers corroborates this. Whenever they wish animals to increase in weight rapidly they pen them up. They have found that the same amount of food will fatten slowly or not at all when the animals are permitted a large range. This same idea is also advanced in poultry raising and production. It seems to me from the experiments on the albino rats that there are good grounds for such ideas. However, one must not lose sight of the product desired. If weight and rapid growth are desired feed the animal in close confinement. If agility and ability to perform work and endure fatigue are wished allow the animal considerable range which allows normal daily exercise.

TABLE V

SHOWING THE WEIGHT IN GRAMS, THE AGE AND THE AVERAGE WEIGHT AND AGE AT THE BEGINNING OF THE EXPERIMENT, THE PRIME OF LIFE AND THE DEATH OF EACH INDIVIDUAL

	YOUNG						AT MAXIMUM WEIGHT						AT DEATH					
									Male Average		Female Average				Male Average		Female Average	
	No. Rat	Sex	Weight in Grams	Age in Days	Male Avg.	Female Avg.	Weight in Grams	Age in Days	Weight in Grs.	Age in Days	Weight in Grs.	Age in Days	Weight in Grams	Age in Days	Weight in Grs.	Age in Days	Weight in Grs.	Age in Days
Exercised Rats	1	M	42	30	41	37	252	544	262	534	176	509	214	746	212	819	128	1014
	2	M	43	30			272	497					206	925				
	3	F	37	30			176	509					128	1014				
	4	M	39	30			261	560					215	785				
Control Rats	9	M	34	30	41	39	310	392	320	391	200	337	*247	1074	241	1222	135	360
	10	M	45	30			331	392					165	1361				
	11	F	39	30			200	337					135	†360				
	12	M	45	30			319	390					172	1232				

* This weight was taken 14 days prior to death and is therefore heavier than it should be.

† Was killed because of sickness.

By consulting Table V and Figs. 13 and 14 it is readily seen that the greatest weight is attained at an earlier age by the control rats than by the exercised ones. The control males reached their greatest average weight of 320 grams at the average age of 391 days. It took the exercised male rats 534 days to reach their average maximum weight of 262 grams. The differences in weights and ages at death are also very pronounced.

Just how much work the control rats would have been able to perform at a given age and how it would have compared with that of the exercised rats at the same age can not be stated as it was not tested. But it is generally conceded that animals kept in close confinement, without a ready means of exercise, can not perform as much work and are much less agile than those having the chance of exercise.

So far as health is concerned it appeared that both control and exercised rats were in the best of physical condition. There was, however, a marked difference in the general behavior and attitude of the two groups. The control rats were slow in their movements, sluggish in appearance and seemed to lack energy, snap, and alertness. The exercised rats, on the other hand, were the reverse in all these respects. They were quick and very agile, bright in appearance, full of vim and very alert. Since these two groups of animals had the same food and practically the same environment it appears that the absence of a ready means of exercise on the one hand and the presence of it on the other is an important factor in causing this marked difference. Again the presence of exercise seems to be one of the causes for the difference in length of life of the two groups. Apparently the rats in the revolving cages not only used up some of the energy in exercise which would have gone into growth, but have also used up some of the energy which would have lengthened their lives.

A slight modification in the environment may probably have been instrumental in causing a difference in the length of life, possibly also of growth. The control rats were furnished with a large bunch of excelsior which they would fashion into a nest. The character of the nest depended upon the temperature. In cold weather the nest would be completely surrounded and covered over having a little tunnel for entrance, but in warm weather it would be open at the top. In this manner of living these rats had always an abundance of fresh air. The home of the exercised rat was a tin box with a certain number of ventilating holes through it and an entrance. It was furnished with sawdust and cotton for a nest. These rats were, therefore, more closely confined during their sleeping time than the control. The air was not so fresh and so free from odors. In fact it was hard to keep these boxes clean. These modifications in environment I think had probably something to do with the differences in growth and length of life in these two groups of animals.

CONCLUSIONS

From the foregoing experiments and data I think the following conclusions can be reached concerning the activity, growth and longevity of the albino rat.

1. The daily activity increases rapidly during about the first third of its life after which there is a gradual decrease until its death.
2. The change in amount of daily activity is not gradual but is rhythmic in character.
3. The character of activity during youth and old age is quite similar, being more or less distributed throughout the 24 hours. During the prime of life the activity is confined principally to night and rest to day time. In other words, the albino rat is nocturnal.
4. The female is much more active than the male.
5. Of the whole amount of work done during the life time almost three-fourths is done before reaching middle age. During the last 30 per cent of life only one-eighth of the total work was performed. During the first 30 per cent of lifespan almost three-eighths of the total work was done.
6. The males far surpass the females in weight.
7. The control males not only reach their maximum weight at an earlier age than the exercised males, but also greatly excel them.
8. The control rats lived longer than the exercised rats.
9. The exercised rats are more active, more alert and brighter in appearance than the control ones.

A NOTE ON THE RELATIVE VALUE OF PUNISHMENT AND REWARD AS MOTIVES

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Two figures

In his book on the dancing mouse, Yerkes[1] says, "The desire for food is unsatisfactory as a motive in animal behavior work, first, because a condition of utter hunger is unfavorable for the performance of complex acts; second, because it is impossible to control the strength of the motive, and finally, because it is an inhumane method of experimentation. In general, the method of punishment is more satisfactory than the method of reward, because it can be controlled to a greater extent." Since a large number of experiments in animal behavior have been made with the use of either punishment alone or with food alone as a motive, it seemed desirable to compare under uniform experimental conditions the relative efficiency of the two methods of training.

The tests described below were made on albino and black-and-white rats. All the rats were given the same problem, namely, to discriminate between two lights of different intensity. Some of the animals were *punished* for *incorrect* choices, and others *rewarded* for *correct* choices. The punishment was a light electric shock; the reward, milk-soaked bread. The rapidity of learning in the two cases was taken as an indication of the value of the method. It seemed desirable to test with still other animals the value of a combination of the two methods—*punishment* and *reward.*

The apparatus consisted of a discrimination-box (see Fig. 1), similar to the well-known box of Yerkes. The rat to be tested was placed in A, and the door I, leading into compartment B, was opened by the experimenter. After the animal had entered B, the door I was closed. The only way in which the animal could return to A was by passing through the compartments W or W′, thence through the corresponding doors V or V′ and into the alleys which open into A at O and O′. The door between the alley and compartment A was opened for the animal the moment it sought to enter A. The floors of W and W′ were wired to form a punishment grill, the two poles of

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[1] R. M. Yerkes. The Dancing Mouse. New York: The Macmillan Co., 1908.

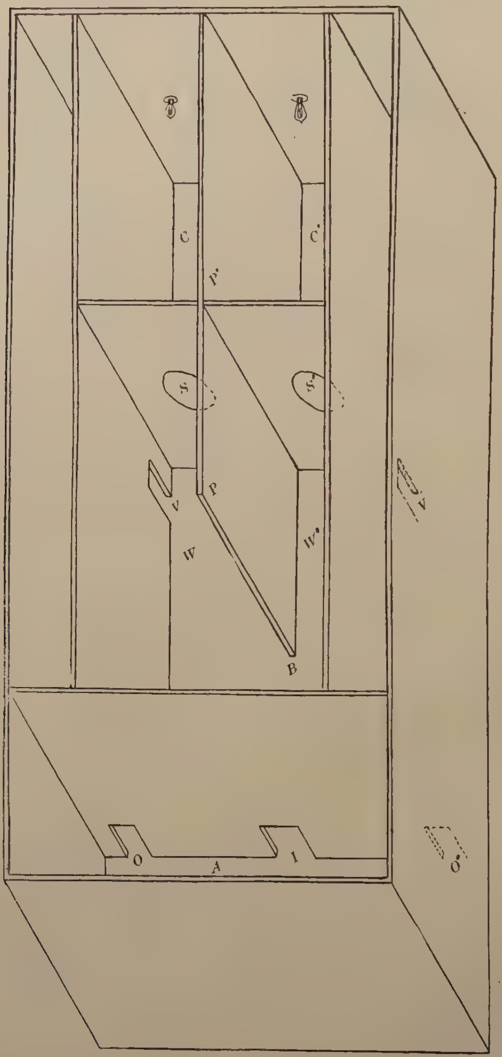

Figure 1. Discrimination box (after Professor Yerkes). A, nest-box; I, door leading into entrance chamber B. The floor of the compartments W and W′ are wired to give electric shock. P, partition between the two compartments; V, V′, doors leading into alleys which have doors O and O′ leading back into compartment. A, C and C′ are the light chambers, never entered by the rats. These are separated by the partition P′. The two chambers are light-tight and were kept tightly covered during test. S and S′ are the standard stimulus plates.

which were connected with a Porter inductorium. A convenient switch enabled the operator to cause the current to flow either through W or W′. Two Columbia dry cells No. 6 furnished the primary circuit. The position of the secondary coil was fixed at 7 cm. The stimulus lights consisted of two uncalibrated carbon lamps, 115 D. C., of 2 and 16 c. p. respectively, placed in the light compartments C and C′. The partition separating B from C contained two standard stimulus plates, S and S′, 5.5 cm. in diameter, placed 25 cm. between centers. The distance between the center of the plate and the floor of the box was 10 cm. Both plates were covered with flashed glass as recommended in the report of Yerkes and Watson.[1]

The tests were made upon light-adapted animals in a room the general illumination of which barely sufficed to show the movements of the animals.

Six female rats were used in the experiment. Five of them, Nos. 1, 3, 5, 7 and 9, were hybrid, and all from the same litter. Nos. 1 and 5 were albinos; 3, 7 and 9 were black-and-white rats, with pigmented eyes. No. 11 was a pure white rat from another litter. Preliminary experiments were begun upon the rats when they were 49 days old. All the rats were allowed to explore the experiment box for two days before preference tests were begun. In conducting the preference tests, 10 trials a day were given each ~~rat.~~ The experimental conditions of the preference tests were made the same for all the animals. At every trial food was placed in a small dish in each of the alleys V and V′. The lights were interchanged frequently and at irregular intervals, in order to exclude choice by position. The two lights occupied the two positions left and right an equal number of times. The two lights are designated, the one as b (brighter, 16 c. p.), the other as d (darker, 2 c. p.). Table I shows the record of the choices made by the animals.

From this table it will be seen that two rats had no preference; that one had a slight preference for the darker compartment, whereas three showed a preference for the brighter of the two.

In accordance with the generally accepted method of training against a preference, those rats which had been found in the preliminary tests to choose the brighter of the compartments,

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[1] Methods of studying vision in animals. Behavior Monographs, No. 2, 1911.

TABLE I

Rat	1	3	5	7[1]	9[1]	11
No. of trials	50	50	50	104	124	46
Choices of b	25	25	22	57	72	29
Choices of d	25	25	28	47	52	17
Preference	None	None	d	b	b	b

were made in the discrimination tests to choose the darker, and vice versa. In forming two of the groups the rats which showed no preference were grouped with those which had shown a preference. Three groups of two individuals each were formed. Each group of two contained one albino and one black-and-white rat with pigmented eyes. The following table shows the composition of the groups:

Group 1. *Punished* after choosing d and *rewarded* after choosing b. Contained—

Rat	1, Albino.	No preference.
"	5, Pigmented eyes.	Preference for d.

Group 2. *Punished* after choosing b. Contained—

Rat	3, Albino.	No preference.
"	7, Pigmented eyes.	Preference for b.

Group 3. *Rewarded* after choosing d. Contained—

Rat	9, Pigmented eyes.	Preference for b.
"	11, Albino.	" " b.

Group 2 was never rewarded. However, since the rats in this group showed great hesitation in entering B after having been punished a few times, they were occasionally fed in A, sometimes after a correct choice and sometimes after an incorrect choice.[2]

RESULTS

Table II shows the records made by the six rats. Each determination represents the percentage of error for a series of 10 trials. Ten trials a day were usually given. If, however, a rat made 10 correct choices during one day, he was given five more

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[1] Rats 7 and 9 were given a greater number of trials because it was found after the first 50 tests had been made that the two lights had not occupied the two positions an equal number of times. The extra trials were given in order to realize this condition.

[2] Several check tests were made in the course of all these experiments, which made it evident that the discrimination was effected by vision alone (by difference in intensity and possibly in color.)

TABLE 2

Percentages of Error for Daily Series of 10 Trials Each

No. of Ser.	Group I		Group II		Group III		No. of Ser.	Group I		Group II		Group III	
	Rat 1	Rat 5	Rat 3	Rat 7	Rat 9	Rat 11		Rat 1	Rat 5	Rat 3	Rat 7	Rat 9	Rat 11
1	30	50	50	50	40	50	**32**	10	20	30	20	30	30
2	40	50	30	60	30	50	**33**	10	20	40	40	30	40
3	50	50	40	50	40	40	**34**	0	30	30	20	50	40
4	40	40	50	50	50	70	**35**	10	10	50	20	40	50
5	20	40	60	60	30	30	**36**	20	20	30	20	30	30
6	50	40	40	60	60	50	**37**	0	10	10	0	10	50
7	40	60	70	60	40	50	**38**	10	10	80	10	40	50
8	40	50	40	80	50	60	**39**	50	20	30	10	50	20
9	50	50	60	50	30	40	**40**	0	20	20	20	30	50
10	60	30	20	40	60	40	**41**	10	10	10	30	20	40
11	50	40	60	50	60	30	**42**	40	30	20	10	40	40
12	30	20	40	30	50	30	**43**	0	60	20	40	40	30
13	40	40	30	80	40	40	**44**	0	10	60	10	30	30
14	40	40	30	50	40	40	**45**	20	10	20	20	30	40
15	30	20	30	30	50	40	**46**	20	10	10	10	30	40
16	20	20	30	50	40	30	**47**	0	20	20	10	40	30
17	30	50	30	30	40	50	**48**	0	0	20	20	20	30
18	30	30	10	30	30	40	**49**	0	20	20	20	20	40
19	30	30	50	10	60	20	**50**		0	20	0	40	30
20	30	50	30	20	20	50	**51**		0	20	0	30	10
21	40	30	20	40	30	30	**52**		20	10	30	20	40
22	20	30	20	20	30	30	**53**		0	0	10	20	30
23	30	50	30	40	30	40	**54**		0	0	10	20	20
24	50	40	60	20	40	20	**55**		0	0	20	30	30
25	20	20	70	20	30	10	**56**				30	20	50
26	30	40	30	50	30	50	**57**				20	30	20
27	20	30	40	20	30	40	**58**				30	30	30
28	40	40	30	20	50	30	**59**				40	10	20
29	20	10	50	20	50	30	**60**				20		
30	0	30	60	20	20	40	**61**				0		
31	0	40	60	20	40	50	**62**				10		

trials. When a perfect record for two days, i.e., 30 consecutive correct choices, had been made, the problem was regarded as learned. The table and curves show that the rats varied considerably in their daily record, as well as in the time required to learn the problem completely. Rat 1 (albino, group 1, *punished* and *rewarded*) completed the association in 490 trials. Rat 5 (pigmented eyes, of the same group), in 550 trials. Rat 3 (albino, group 2, *punished*) learned the problem in 550 trials, but rat 7 (pigmented eyes, group 2) had not learned the problem in 620 trials, at which time the work had to be discontinued. Neither of the rats in group 3 (*rewarded*) learned the problem in 590 trials, at which time work had to be discontinued with them also. The table shows also that the rats exhibited great instability even until the end of the experiment. A comparison of the errors of rats 3 and 7 shows that rat 3 had never made a wholly perfect series of records before her 520th trial, whereas rat 7 had made several perfect daily records before the 30 errorless choices were made in succession.

Fig. 2 shows the error curves for the three groups. The ordinates represent the percentage of error; the abscissae the number of groups of 10 trials each. It will be seen from these curves that group 1, which was both *punished* and *rewarded*, was the only group in which both rats made the discrimination. The curve of the *punished* group approaches that of group 1 more nearly than does the curve of the *rewarded* group, since one individual of the *punished* group learned the problem.

Several interesting observations were made during the work. The rats of the several groups maintained different attitudes toward the work. Those animals which received the electric shock showed after a few trials great hesitation before entering B, whereas the rats of group 3, which were never shocked, rushed into B without making any apparent choice. The rats which were punished became unwilling after a time to enter the electric box, and they assiduously avoided the door to this compartment, apparently associating the light with the shock. Great patience was often required of the experimenters, as several minutes would sometimes elapse before the rat could be persuaded to come to the door I. When at length it passed its head through this door, it would look to right and left several times before making a choice. This indecision would as often precede an incorrect choice as a correct one. However, as the discrimination became established, the animal ceased to fear to enter the electric compartment. It would come to the door I, glance only once to left and to right, and then dart toward the correct light. Although the rats which received punishment were at first unwilling to enter the electric compartment, they never became sulky as did the turtles used by Casteel.[1] The rats remained in good condition throughout

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[1] D. B. Casteel. The discriminative ability of the painted turtle. *Jour. of Animal Behavior,* 1911, vol. 1, no. 1.

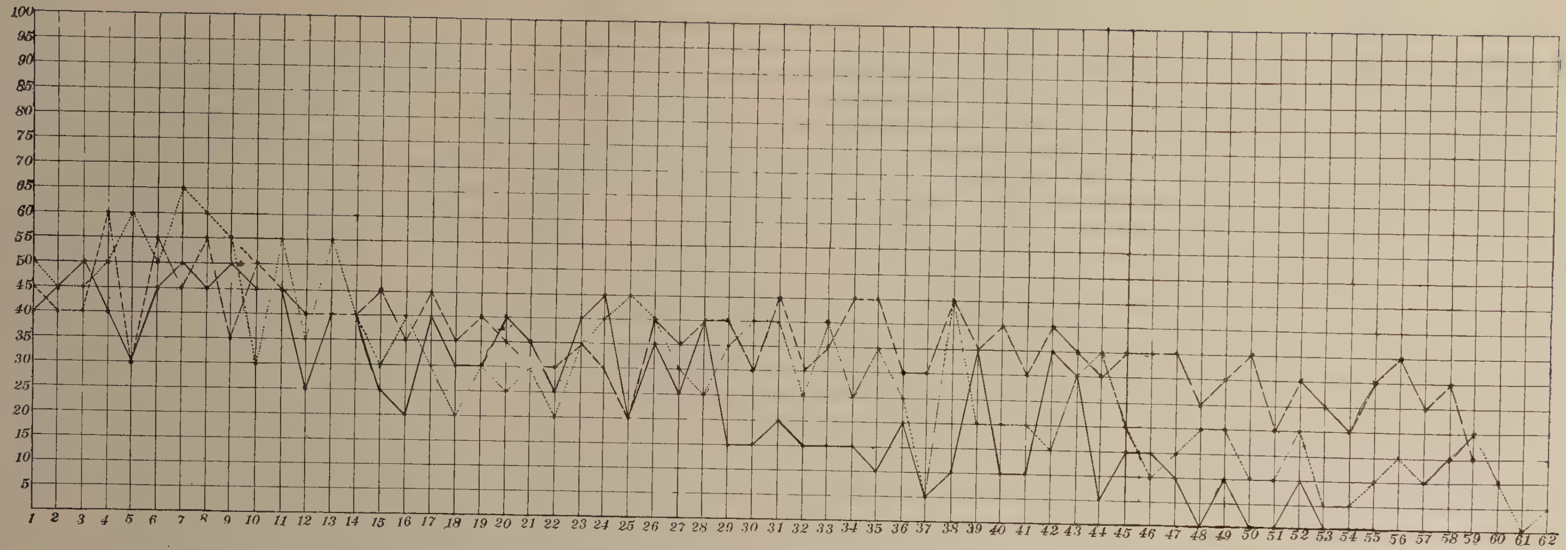

FIGURE 2. Error curves plotted from the data given in Table II. The numerals in the left margin indicate the percentage of error; those below the base line the number of the series, each series consisting of ten consecutive trials. The solid line (————) is the error curve of Group I (rewarded and punished); the dotted line(. . . . .) is the error curve of Group II (punished); the dashed line (– – – – – – –) is the error curve of Group III (rewarded).

the experiment. Except for the nervousness referred to above, none of the animals experienced any ill effect from the work, and no differences in the general health and activity of the three groups were observed.

The failure of the rewarded rats to learn the problem in the time allowed is of particular interest, since their preliminary work (preference tests) was along the same line as the work of the problem; whereas, in the case of the rats which were punished, a new element, the electric shock, was introduced.

The difference in the rate of visual discrimination between albinos and rats with pigmented eyes deserves notice. In each group the white rat made the discrimination before the rat with pigmented eyes. This is apparently not in harmony with the results obtained by Karl Waugh,[6] who states that "the discrimination of the albino mouse is not so good as that of the mouse with pigmented eyes." In neither the work of Dr. Waugh nor in the present work were a sufficient number of animals used to settle the question of the relative discriminative ability of the two varieties.

It seems evident from this experiment that a *combination* of *punishment* and *reward-motives* is more effective in bringing about visual discrimination in the rat than is either punishment or reward used alone. It seems evident, also, that punishment is more effective than reward, at least in so far as the rate of learning is concerned.

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[6] Karl Waugh. The rôle of vision in the mental life of the mouse. *Jour. Comp. Neurol. and Psychol.*, 1910, vol. 20, pp. 549-600.

BEHAVIOR AND COLOR CHANGES OF TREE FROGS

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INTRODUCTORY

Concerning the general facts of the life history, behavior, etc., of amphibia as a class much is well known. The admirable "Frog Book," by Miss Dickerson ('06) has made available a splendid body of information concerning "North American Toads and Frogs," and a similar service has been rendered by Boulenger ('98) in the "Tailless Bactrachians of Europe." But admirable as these are for the general student, they leave much to be desired in the way of detailed scientific investigation. This is particularly the case with phases of behavior, color changes, development, etc.

In the following account I have sought to bring together the results of observations and experiments touching facts of behavior and color changes in two species of tree frogs, *Hyla versicolor* and *H. arborea;* the former, the common tree frog of eastern North America, the latter the equally familiar tree frog of Europe. My study of *Hyla arborea* has been limited to about two months, and was done at Naples. In the case of *H. versicolor* my observations cover a period of several years, though at such incidental times as made it convenient and practicable. As will be seen, these studies include both field and laboratory work, especially of the American species, and I have made the field work emphatic wherever at all practicable. I have elsewhere ('09, p. 157) emphasized the crying need for larger attention to this phase of experimental work, believing that in many cases it is all but impossible to secure trustworthy results as to behavior of animals where the work has been done under such unusual, unnatural and artificial conditions as most laboratory provisions afford.

What right has one to assume that the actions of an animal taken rudely from its natural habitat and as rudely imprisoned in some improvised cage are in any scientific sense an expression of its normal behavior, either physical or psychical? Is it within the range of the calculus of probability that conclusions drawn from observations made upon an animal in the shallow confines of a finger-bowl, but whose habitat has been the open sea, are wholly trustworthy? It is no part of my purpose to discredit the laboratory or laboratory appliances as related to such investigations. They are indispensable. But at the same time let it be recognized that they are at best but artificial makeshifts whose values, unless checked up by constant appeal to nature, must be taken at something of discount. This must be especially the case with higher organisms. Some of these may, of course, be readily domesticated, or made more or less at home in aquaria or vivaria; but not a few absolutely fret their lives out, are never at ease, and probably never give expression to a natural reaction under such conditions. It seems to the writer that until one has been able to place his specimens under conditions approximating the natural, or has at least brought them to a state of semi-domestication, where in food-taking, evidence of health, etc., they are at ease, he has small right to dogmatize as to conclusions, or presume to make such conclusions the basis of so-called *laws of behavior*. Not a little of recent investigation along the lines of behavior has been vitiated at just this point, and must be repeated to be made trustworthy. The amazing mass of contradictory results which has loaded the literature of recent years is attributable to some extent to this misfortune.

In the following account the above precautions have been in constant mind, though owing to the peculiar habitats of these animals it has been attended with peculiar difficulties. In many cases it has been quite necessary to subject my specimens to laboratory conditions; but even then care was taken to simulate as far as practicable a natural environment. In certain cases this was done by enclosing a shrub by a fine meshed net, and thus leaving it almost exactly as if at home; and in all cases much attention was devoted to having specimens provided with leaves, moisture, etc., and with a supply of insect food, which afforded an approximation to natural surroundings. But even so, it is freely admitted that at best they are not wholly at ease; and behavior must not be too dogmatically interpreted.

BEHAVIOR

It may be assumed that in general tree frogs share about the same measure of intelligence as other members of the amphibian tribe. But even this would not place them high in that rank; for at the most favorable estimate amphibia are not credited with a large measure of mentality. But it may be doubted whether in general tree frogs may even claim so high a degree of intelligence, judged by their behavior, as many of their kin. It may be the peculiarity of habitat has induced a degree of stupidity in relation to danger from enemies, or possibly the color adaptations of certain species may have had something to do in this matter; but certain it is that they show less wariness or alertness than do the frogs whose habitat is upon the ground. In some other respects, however, they show a degree of cleverness which is not noticeable in the latter. For example, the facility with which they may leap and capture prey is quite remarkable. Again, the accuracy with which they seem to gauge distance is also striking. So that altogether it may be assumed that in rank of intelligence they are fairly comparable with their fellows of other genera and species.

The features of behavior which have had more particular attention are three, or perhaps four, namely: food-taking; light reactions; temperature reactions; hibernation. Since the last is largely a question of temperature it might perhaps be considered under that head. However, my observations on this feature are comparatively few and may as well be disposed of in this connection.

FOOD TAKING

In this Hyla behaves quite similarly to others of its kind. It seems not to notice any except moving objects. A spider may remain quietly in a given part of the cage for hours or days undisturbed. If it assume an active attitude it is almost certain to be taken very promptly. It is thus with any prey. The insects most commonly supplied were flies, small beetles, grasshoppers, spiders, etc. On one occasion a small wasp was released in the cage and at once began to buzz about or run up the sides of the cage actively. It was but a few moments ere a specimen leaped eagerly and captured the prey. Then a most interesting performance took place. No sooner was the wasp seized than it was whipped into the mouth, and in turn stung the frog; the frog in turn showed a very lively appreciation of that fact, and made an apparent effort to eject the creature; but the process of ingestion had gone too far, and deglutition was completed without further ado, nor did the frog show the least further sign of distress. On another day the operation was repeated and very much after the fashion of the preceding. It may be doubted whether amphibia show any particular discrimination based on that type of experience.

An interesting feature exhibited by Hyla was that of leaping to take its prey. Seldom does it show any disposition to stalk its prey, as do others of the class. It seems rather to wait till the prey is within leaping distance, which may mean several feet, and then with an easy spring it takes the victim with great accuracy, nor does it ever fail, so far I have seen, to safely lodge in a safe place. It seems not to detect prey at close range. I have seen, repeatedly, insects run over the body or legs of the frog, or indeed over its head and mouth, without a sign of recognition on the part of the frog. But let it be seen at some distance and the whole behavior changes at once.

Hylas are voracious feeders, and digestion seems to be fairly rapid though not very complete. It is quite easy to recognize in the feces the nature of the food taken. For example, a digested grasshopper is a *grasshopper still*! And so with a beetle or other insect. The chitinous exoskeleton seems only to have been softened and the internal proteid and other food elements to have been extracted and assimilated.

HIBERNATION

Presumably hibernation is a more or less similar phenomenon among all amphibia. In general its chief features are quite well understood. On this point my observations on species of Hyla add little that is new. Its first indication is expressed in a tendency to escape from unpleasant cold. Specimens in the laboratory show no disposition toward hibernation so long as conditions of temperature are conducive for activity. My specimens were in apparently normal activity during the months of November and December in the laboratory so long as conditions were favorable and food was supplied. The last week of December some five specimens were placed in a cool, damp corner of my cellar and observed from time to time. Very soon after this change they showed signs of dormancy, crept, or rather *backed*, for the mode of burrowing seems to be by means of the hind feet and the sharp posterior end of the body working together. In this way they burrow and bury themselves. My specimens burrowed backward under the moss and debris of the cage, crouched with head close to the bottom, closed the eyes and literally went to sleep. They were left for some time and in March I carefully inspected the box and found that a very small specimen had died. The others seemed normal. They appeared very sluggish, yet when turned over they righted themselves and resumed the sleeping attitude. Toward last of March they were again inspected, and to my great surprise and regret all were dead. Whether the hibernating conditions had proven unsatisfactory, or whether the inspection and handling to which they had earlier been subjected, was the occasion of the untoward ending one may only surmise. Perhaps something of both may have been involved.

Hibernation in a state of nature I have not studied. In one case I was fortunate in finding a specimen which was apparently just emerging from its winter sleep. It was found in the woods and very near where at the same time I found a specimen of the wood frog which had not yet emerged, but seemed in process of emergence, as the specimen was dug out from a bank of earth and leaves, and not yet sufficiently active to make any efforts to escape. In late autumn I have also found specimens on the ground along a wood path, and conditions of temperature were such as to suggest the presumption that they were even then seeking suitable hibernating quarters.

COLOR CHANGES

The general facts of color changes as a feature in the behavior of amphibia have been long known. Of course, tree frogs as affording some of the best illustrations of this phenomenon are no exception to this matter. In fact the European species, *H. arborea*, has been most critically studied of any, and has perhaps afforded the larger mass of existing knowledge on the subject. As will be seen in a later connection, some of the more striking aspects of behavior in color change have been studied in this species. So far as I am aware no one has made any of the

American species the subject of special study in this particular phase of behavior.

I shall begin my account with observations made upon *H. versicolor*, and later take up similar studies of *H. arborea*, with a comparison of the behavior of the two species as relates to color changes.

The present series of studies had their origin in some casual observations made upon *H. versicolor* in the early autumn of 1906, both as to color variations exhibited by specimens under essentially identical conditions of light, temperature, etc., and as to a peculiar habitat that seemed unique. Noting first the matter of habitat it may suffice to merely state the fact that the specimens were found perched upon the black iron fence of a cemetery along which was a cement walk leading to an open field often sought as a collecting ground for various specimens liable to afford laboratory material. The special position of the specimens was upon the flat surface of projecting supports for barbed wires strung above the fence proper. These supports like the other parts of the fence were painted dead black. Evidently they had climbed up the posts from the ground and had found a congenial resting position; but just what may have induced them to choose such a place it is impossible to suggest. But the fact of habitat aside for the time, my next point of curiosity was found in that the first specimen was very light grey in color, appearing almost white in contrast with the black support on which it was reposing. I merely paused to observe the little creature in its novel position, but came close to it to make the inspection exact, but without disturbing it in the least, as it seemed utterly unconcerned and unafraid, blinking sleepily, but without other sign of activity.

Somewhat further along the same course a second specimen was observed in exactly the same general position, perched at ease on the shelf, backed up against the post. In this case the color was very dark, and so in striking contrast to that of the first. As before, I paused for a few minutes and scrutinized the specimen as carefully as I could without actually picking it up, which might easily have been done, for it made not the slightest attempt to evade capture. However, it was passed with nothing beyond the cursory examination mentioned. A few days later I was passing along the same course with a friend, and about the same place found another specimen—possibly one of the same. We paused and I took occasion to point out some of the peculiarities already mentioned. Reflecting on the matter it occurred to me that perhaps some more painstaking observations, or possibly experiments might prove worth while. Accordingly on my next trip that way an observant eye was kept alert to note other specimens. Fortunately four were found, all occupying the same relative positions on different posts, but with the curious difference that no two were of the same color. One was very light, a whitish grey, one green, the other two very dark, one almost black. This was about ten o'clock, on October 10, and the day was bright and warm, all the specimens being in the sun. Following critical study of the specimens in position, they were then taken and carried back to the laboratory for further observations.

On a subsequent trip a few days later, several others were found in same location and always in the same positions and attitude. Of these one specimen was in shade, the others in open sunlight, and all were very light in color. On still later trips others were found, invariably in same general positions. It seemingly made no difference as to the hour of day, whether in sun or shade, whether the day were warm or cool; in almost every instance there was the same diversity of color markings and intensity. It was this seeming anomaly which first enlisted my attention and interest, though the peculiarity of habitat already alluded to was also involved in the interest.

EXPERIMENTS

As already mentioned, one of the first features of the subject to engage my attention was the seemingly extraordinary aspects of color difference characterizing the several specimens found under exactly the same environment. It is now my purpose to briefly describe the observations and experiments by which it was hoped some adequate explanation of the matter might be secured. Repeated field trips were made in order to find, if possible, some clue to the subject by a study of specimens under their natural surroundings.

On a previous page mention has been made of the records of two of these trips. A third trip secured three additional specimens; one was a very light whitish grey with the pigment figure sharply defined, a second was bright diffuse green, the pigment figure more obscure, and the third very dark, slaty brown, the figure pattern obscure. On a still later trip a single specimen was found, and was bright green. The light and position were the same as before. It was taken and carefully wrapped in soft damp paper and carried to the laboratory. When released in the experimental cage a half hour later it was found to have become a very dark, almost black color.

On a following season several trips to same locality resulted in finding some eight new specimens, all occupying the same positions as those of previous year. As before, there were marked differences in coloration. Of three specimens two were in open sunlight, and one in shade under large tree, and all very light whitish in color, with the pigment pattern sharply defined. Of two other specimens taken later one was almost black, the other almost white. The day was warm and bright in late September. In early spring, May, I found a single specimen which had apparently but recently emerged from hibernation. It was almost white, and presented marked contrast with the support upon which it was perched. These were taken to the laboratory as before, but in a closed collecting box and when released were found to be very dark. It should be noted that the last specimen mentioned was taken to my home and its subsequent behavior observed in a cage and in my garden lot.

From this account may be summarized the following: Of the fifteen specimens of which records were made, seven were whitish grey to pale grey; two were bright green; two very dark brownish; four slaty to blackish. This does not include several other specimens, probably about a dozen, but of these no permanent records were made, and so they are left out of account, except to state the general fact that they shared in general the same color variations exhibited by those more critically studied. It will be observed that we have here a range of color from almost white, through grey, green to yellowish, brown, slaty to almost black. Yet this range was to be observed in specimens occupying the same general positions, the same conditions of light and temperature, the same habitat. It seems rather obvious that the diversity cannot be explained by anything of an environmental nature. As will be seen in the later accounts of experiments similar diversity was evinced under identical tests.

But not only the anomalous color features call for explanation; there is also the hardly less anomalous peculiarity of habitat already referred to, which likewise is a matter of behavior the meaning of which is not at all obvious. I do not forget that occasionally these creatures may be found on old fences or walls. Still it is exceedingly rare to find them in such places. In all my observations, covering many years in a general way, only once have I actually found a specimen in such habitat, and then it was on an old rail fence not far from the wood. In this case it was in mid-summer, and the creature seemed quite at home in the devious labyrinths of light and shade, etc. This, however, is quite a different story from that here under review, and still leaves doubtful the why and wherefore.

Of course, the contiguity of the wood-side might suggest the possibility of descent from the trees looking toward hibernation. But when first observed it was in early September while the weather was still very warm, the trees in full foliage, and food quite abundant; too early apparently for the hibernating instinct to manifest itself. Nor could it be prompted by quest after food; for of all places this would seem the most unpromising. Even the elaborate webs of autumnal spiders were conspicuously absent on this fence. Nor on the other hand, could it have been prompted by unusual satiety of appetite, for when placed in the cages they were quite ready and eager to take an insect. I merely submit the facts without further comment, and leave the problem open to further light. It may be noted in passing that during one fall not a single specimen was found in this locality, even after diligent search. As hinted above, I am still disposed to regard the matter as in some way, not very clear, related to the approach of the hibernating season, the first expression of which on the part of the frogs would probably be descent from the trees. But even at best this is merely a guess.

In an account of color reaction in which an attempt is made to measure or determine with some approximation the amount of color change which takes place at a given time, or under a given test, it is very desirable that one have some basis of comparison. In the case of Hyla this is somewhat difficult. It has seemed, however, that the pigment patterns on the legs, and especially the dorsum, afford a fairly good basis. It seems quite as decisive as that of the lateral spines of the lizard, Phrynosoma, which Parker ('06) employed in his experiments. I regret not to have secured successful photographs of extremes in either direction; such figures are, however, admirably shown in "The Frog Book," Pl. XLVI.

As to the chemistry or mechanics of color change I shall not attempt a formal discussion or explanation. Those who are concerned with this feature may find extended details in the paper of Biedermann ('92), or in the paper of Parker (op. cit.). It may suffice here to merely say that skin color is due to the presence in the derma of certain pigment granules, usually contained in large pigment cells known as chromatophores, melanophores, etc. These granules are capable of migration distally, that is, toward the surface, or in the opposite direction, under certain stimuli. Certain other cells of the epidermis or subepidermis, known as guanin cells, form a reflecting layer which, on the contraction of the chromatophores act as a screen to obscure the pigment and at the same time reflect from their surface light falling upon it from outside. In a word, then, the distal migration of the chromatophores accentuates the appropriate color, while the migration in the opposite, or proximal direction decreases the color elements, and the guanin layer reflects the lighter color of its own cells.

In the laboratory the first attempt was to test the effects of light in relation to color. In the first series of tests five specimens were used, which were placed in glass jars of about two or three gallons capacity, perhaps nine inches in diameter by 15 inches high. Into one of these damp moss was placed, and in the other a branch with lateral twigs, and the tops closed by wire screens. These cages were at first kept in my private laboratory where a fairly uniform temperature was maintained, and where was a good diffused light from north windows. For experiments with direct sunlight the specimens were carried into an adjacent laboratory having east windows. The first experiments were simply the transfer of a cage from a remote and darker part of the room to a table close to the window, or even upon the ledge of the window. My records show a general lightening of the skin color as a result; but as will be seen later this inference was perhaps incorrectly attributable to the sole effect of light intensity.

To test the effects of direct sunlight the cages were taken from the diffuse light and placed on the table in direct sun. As a rule this had the effect of a rapid lightening of the skin, and the gradual fading of the pigment patterns of both legs and back. One of the specimens in this case rapidly assumed a green color in the light of the sun, while the other became whitish-grey. This experiment was made at nine o'clock and at two o'clock the green color persisted in the one, while the other specimen had become very dark, even darker than at the time of the test.

This experiment with direct sun was repeated many times in the course of the following few days, and usually with the same result, viz., the rapid lightening of coloration. It must be stated, however, that the green color was exceptional, and when it occurred was more persistent. In one case to be noticed later this green color became singularly permanent under a wide range of experiments, continuing over several days.

The next experiment consisted of putting one cage under a black hood, while the other was left as a control in the diffuse light of the room. After an hour the hood was removed but not the slightest change of color had taken place. Like the preceding experiment, this was repeated many times but with almost uniformly negative results. This seems in rather marked contrast with that associated with the capture of specimens and their transfer in the dark collecting box to the laboratory, in which the very opposite was usual, viz., the darkening of the skin. This also will be further considered in a later connection.

Two further experiments along this line are rather important. First may be mentioned the specimen taken in early spring, referred to in an earlier connection. This specimen when taken was of the usual whitish grey color. It was carried home from the woods and kept in an open jar on a back porch free from interruption. Experiments as to its light reaction seemed very prompt and more than usually positive. In a bright diffuse light it rapidly became light in color. Placed under a very dark hood for half an hour it had resumed the dark slaty color. The hood being removed a rapid lightening of the skin was very evident. The experiment was repeated several times and with similar results. However, when tried the following day the creature *failed utterly to respond to these tests.* On a still later day I transferred it to a jar into which had been placed a leafy branch and scattered green leaves. In apparent response the specimen gradually assumed a green color which spread over the entire dorsal portion of body and legs, and was most striking. A few hours later the leaves and branch were all removed, but the green color persisted. Repeated experiments of subjecting the specimen to darkness, placing it in open sunlight, change of temperature, etc., were of no avail; the color persisted for more than two weeks without essential variation, save in the matter of intensity. Finally, it was released in a tree in the garden lot and seemed perfectly at home, leaping to catch flies, ants, etc., but still no color change appeared.

A similar case appeared in the following fall. Three specimens were taken, one being green, one quite dark, the third very light. All were placed in an experimental cage and the following day a second had changed to beautiful green. The third day all were green, and so continued for five days. In the meantime another specimen had also been taken and was placed in a separate cage. When taken it was distinctly greenish, though not deeply so. During the process of transfer from field to laboratory it had become very dark, and continued so for an entire day. It then assumed a greenish hue which persisted for several hours, but later was replaced by the dark color. In neither of these had there been any proximity to leaves, or any green body. Details on this point will be submitted in a later connection.

Temperature. The intimate relations of temperature and light reactions have long been known; but only within recent times has this been made a critical study. Parker and Starratt ('04), and later Parker ('06), have shown rather conclusively the importance of both, but especially that of temperature in such behavior. One of the interesting conclusions of these observers is that light and higher temperature act in directly opposite ways, viz., that while light causes a distal migration of pigment and darkness a proximal one, heat on the other hand causes a proximal movement of pigment, and cold a distal one. It follows, on this assumption, that where these factors coöperate, i.e., light and low temperature, darkness and high temperature, we shall have the maximum expressions of the appropriate reaction. To quote directly Parker's statement, "Light causes a distal migration of the pigment granules of these cells; its absence a proximal one. A high temperature causes a proximal migration of pigment; a low temperature a distal one." He believes there are no real exceptions to these rules. I have not experimented with lizards, but from what has already been presented it will be seen that there are among tree-frogs very striking and positive exceptions, and accounts now to be cited will make this quite certain.

In my temperature experiments two chief methods were employed. First, and I think the more satisfactory, was the simple transfer of the cage from the room temperature to that of the outside air, which was easily done by raising the window and quietly lifting the jar from the table and placing it upon the outside window shelf; making accurate records of the temperature in each case. This feature could also be supplemented by utilizing the presence of a temperature oven which was within easy reach of table or window.

The second method, and this proved preferable at Naples, consisted in placing specimens in temperature baths, i. e., by means of ice or heat it was quite possible to have a vessel of water of any desired temperature, into which a specimen could be put and left the desired time without in any serious manner injuring it or interfering with its behavior.

Experiment. A jar containing two specimens was placed on the window shelf where the thermometer registered 14 C. At the end of one and one-half hours both specimens had changed from a dark brownish to very light grey. They were then placed on the inner window shelf where temperature was 21 C. and at the end of half an hour both had resumed the original color. In the room on the same table a control jar with three specimens had remained without change during the same time. The experiment was now reversed, that is, the jar was placed over a radiator shelf where the temperature gradually rose to 35 C. Both specimens showed signs of discomfort, moving about, shifting the body variously, scratching the nose with fore feet, etc., and in the meantime both had become markedly lighter in color, though not equally so. After a half hour the jar was transferred to the outer window shelf where in a half hour the temperature had fallen to 15 C. and both had grown almost white in color. Here we have one of the many examples of color change which negatives Parker's rules. The light throughout had been practically the same; hence the reaction must have been quite apart from any influence from that source.

Experiment. A jar containing three specimens was used, and the room temperature was found to be 21 C. At this the color of two was a grey over back, with distinct green on sides; that of the third distinctly darker and without trace of green. The jar was next placed on outer window shelf where the temperature was 4 C. One of the greenish specimens continued absolutely unchanged; a second became distinctly lighter and the green disappeared; the third remained in same position and color just as at beginning of experiment. After about an hour specimen No. 1 had become distinctly lighter, much like 2.

This experiment was repeated on a subsequent day. At the first, one specimen was very bright diffuse green, the other two were very dark colored. Room temperature about 21 C. The jar was placed on outer shelf where temperature was again 4 C. They remained here for more than half an hour and with only this color change, viz., the green specimen had become greener, the color having extended to the legs and become more intense. The color of the others had remained as at the beginning.

These experiments were variously repeated on these specimens, but in the same general manner, and with results so similar as to call for no special account. The following observations may be noted. On one day in early morning the temperature of the room had fallen quite lower than usual, viz., 12 C. Two frogs were found crouched under the moss and both very light, whitish grey; a third was crouched on top of the moss and very uniformly dark over body and legs. In the afternoon they were again observed, the temperature having become about normal, 20 degrees, and while all had continued in same positions, the two under the moss had become quite darkly colored, the other remaining as before.

Other temperature experiments will be described in connection with the account of *H. arborea*, and any special remarks and discussion may be deferred to a later time. Enough has been submitted, however, to confirm the suggestion made in an earlier part of this section that these frogs fail to sustain the theoretical rules.

Other experiments. In connection with the preceding observations and tests it was noticed in several instances that the mere handling of specimens often had the effect of involving color changes quite as marked as any of those already described. For example, in several instances it was noted that in carrying a cage of specimens from one room to another a perfectly evident color change was induced. To test this careful attention was given to color patterns of specimens in perfect quiet by two or three observers. Then a cage would be taken up and turned about, lifted up and then returned, etc., etc. Then another careful scrutiny would be made; and it soon became evident that almost any such disturbance might act as a stimulus. I even tried the effect of merely close scrutiny without any jostling or moving of the jars, and found that where a specimen could be brought to *observe* that it was observed, there was often a color change quite as evident as the others.

The following experiment will show that a mere stimulus is not of itself always sufficient to arouse a color reaction. I introduced the electrodes of a battery into a cage in such manner as to enable me to apply them to a specimen almost at pleasure. I was able thus to compel the specimen to leap vigorously about the cage for some time. But this was apparently without direct effect on coloration. This was the more surprising as other experiments of mechanical irritation with needle or forceps had *seemed* to act to induce a darkening of the skin. But similar experiments on *H. arborea* were frequently negative, hence it may be regarded as doubtful whether such stimuli serve to influence to any appreciable degree the coloration.

This does not, it seems to me, discredit the suggestion as to the fact of a nervous, or emotional factor as involved in these phases of behavior. So far to the contrary I am disposed to believe that we have here one of the important elements, possibly the *most directly* important, involved in this class of behavior. With this in mind one may seriously question whether the marked color changes almost always associated with the capture and carrying of specimens to the laboratory be not an expression of the *emotional* condition of the animal, rather than the mechanical effect of darkness, or other physical agent.

In this connection may be mentioned the case of one specimen which was taken in the wood and brought to my home. When taken it had been of the usual whitish grey coloration; but when taken from my box and placed in a large glass fruit jar it was very dark, almost black. Exposed to the light on the open piazza it very soon became very light colored. Covered with a black hood for half an hour it was found to have again become very dark. On exposure to light the whitish color reappeared. This was several times repeated and with similar results. Similar experiments the following day, and on subsequent days, failed utterly to show similar reactions. May one venture the suggestion that the creature had acquired such familiarity with conditions as to dissipate to a degree its emotional sensitiveness?

HYLA ARBOREA

During my recent occupancy of the Smithsonian Table at Naples, for the courtesy of which my acknowledgment is herewith tendered, I was fortunate in securing through the laboratory staff, some twenty specimens of this beautiful tree-frog, and was able to keep them under observation for an entire month. Normally this species is a bright green color over the back and sides and legs, while below it is pale pinkish to salmon color, with a black line extending from the eye along the side to the base of the leg. Considerable differences, or color variations are frequent and have been the occasion of several proposed species, as may be seen from any casual review of the systematic literature. (Cf. Boulenger, The Tailless Batrachians of Europe, p. 250.)

It need hardly be said that the color changes of this species has had considerable attention by many observers; but as is the case with the previous species, it has been for the most part rather general. So far as I am aware, the most critical and detailed investigations are those of Biedermann ('92). While very much in the results of this investigator must have an abiding value, especially those features dealing with the chemistry and mechanics of color phenomena, still there are others which have been questioned, and which I have not been able to confirm in the course of my studies. To certain of these I shall have occasion to refer repeatedly in what is to follow.

By way of introduction to this phase of my problem let it be said that, while many points of difference will be found as the two species are compared, I have been somewhat surprised in noting the many features of agreement which have come to light in their comparison. *Hyla arborea* shows the same individuality of behavior as does *H. versicolor;* it also exhibits the same erratic aspects of color reaction which have already been passed in review. From Biedermann's account I had confidently anticipated a degree of constancy in behavior which has not been realized under actual experiment. Let it be noted that my observations on this species have been restricted to the laboratory. I have not studied it in nature. Again, my work has been limited to a comparatively brief period, and to a single season. Except for the previous work with the former species I should feel less confidence in the results relating to the latter.

Two rather primary objects prompted my experiments on this species: First, a desire to compare its behavior with that of *H. versicolor;* and second, a review of the experiments and conclusions of Biedermann. As a preliminary to the latter it may be well to briefly summarize some of the more fundamental of his methods and results, but only in so far as they pertain to color changes. Furthermore, I shall not concern myself with the elaborate chemical details which occupy a large place in his investigations.

It has long been held, following the experiments of Lister ('58), that the nervous system was directly involved in these color changes, and further that they were under control of the animal, and operative only through the sense of sight. This view is held also by Boulenger ('97), who says, "That these rapid color changes harmonize, within certain limits, with the surroundings, is well known. The researches of Dutartre on *Rana esculenta* have shown that the changes are controlled by the animal, the contraction and expansion of the chromatophores not being due entirely to the direct action of light and moisture upon the skin, but also to a reflex action of the sympathetic nervous system brought about by the visual impression. Comparative experiments conducted on frogs possessed or deprived of the sense of sight, and placed in different conditions of light, show the blind individuals to change color much less rapidly." (p. 25).

Biedermann also admits the influence of the nervous system in relation to these changes, but holds it to be due to reflexes other than visual, contrary to the view of Leydig who holds with the foregoing to the direct influence of the visual reflex. According to Biedermann it is perfectly easy to bring about such changes of color by modification of conditions which affect contact stimuli. For example, according to his experiments, all that is essential in the case is that the surface be *smooth* or *rough*, or that conditions which involve such sensation be induced. This latter he held might be possible by section of the nerves of the foot, or by drying the foot and thus disturbing its normal sensory function. From experiments subsequently described it will be noted that these views have not been confirmed.

In my account of the many and varied experiments carried on during March and April at the Naples Zoological Station, I shall give in detail only those which have the most direct bearing on the special problem of color change. Naturally I was first concerned with those features which had been made prominent by Biedermann, as mentioned above. Among several kinds of cages or receptacles employed in the experiments, only two were found generally useful, viz., glass jars of some six liters capacity, and cages of wire gauze having a zinc bottom to afford means of supplying needed moisture, and a glass front to facilitate observation. Both were convenient alike for experiment and observation, but specimens seemed invariably more at home in the jars than in the cages, a matter of no small importance, and hence these were used for the most part.

Contact stimuli. As stated above, Biedermann has emphasized the importance of the nature of the stimuli acting upon the sensory nerve endings of the toes as determining factors in color changes in these creatures. It is in this way that he explains the reactions following the introduction of leaves into the vessel. " Wählt man nur solche aus und bringt sie (in dunkeln) in ein anderes Gefäss mit Pflanzenblättern zusammen, so ergrünt die Haut in kurzester Zeit. Der Versuch gelingt auch mit künstlichen Blättern und es beweist dieser Umstand allein schon, dass als auslösender Reiz wohl nur gewisse Berührungsempfindungen in Betracht kommen." (p. 506).

It will be noticed that this experiment was conducted in darkness, thus excluding the influence of either light or vision. By two other forms of experiment he claimed to demonstrate that by contact with a rough surface a darkening of the skin was produced, even to complete blackening. So simple seemed the experiments that no time was spared in putting them to the test. Accordingly I sought to duplicate the experiments, and placed the same number of frogs in the wire cage, the bottom of which was covered with a very coarse jute matting, and in the glass jar. After several hours under these conditions the only difference appreciable was that the color of most of those in the jar was definitely darker than those in the cage; just the reverse of what should have been the case. To vary the experiment a glass jar was prepared by enclosing a coarse wire netting over the sides, and coarse blotting paper over the bottom. Into this several specimens were placed and left for several hours, but all the while under critical observation. It was not possible to distinguish the slightest indication of color change. The jar was then placed under a black hood and again left for an hour. In one or two cases there seemed to be a slight darkening of the green, but it was not marked. The question of the influence of darkness will be considered in another section.

I next tried the experiment with leaves. Several of the darkest specimens were placed in a jar in which had been arranged a leafy branch and leaves scattered over the bottom. Two at once took up a position on the leaves, two clung to the sides of the jar, and one remained on the bottom. They were watched critically for two hours, but with only negative results, no change of color occurring. Next the experiment was tried of putting a jar of these specimens in a cool, dark room over night and early the following morning introducing into the jar a leafy branch and leaving in the dark for some hours. As before, the result was wholly negative. The experiment was varied by using the wire cage and a smooth glass jar each with the same number of specimens and leaving both in the same conditions of light and temperature during an entire forenoon. At the end it was found that in each case there were some specimens light green, some darker green, some very dark olivaceous. But it was not possible to distinguish that any significance attached to the nature of the cage or receptacle, or that conditions of contact could have played any rôle.

In the next place experiments were made to test the part played by the feet or toes as sensory agents. A specimen was placed in a very dry jar lined with white blotting paper, after having dried the animal very thoroughly with a dry towel. Another was similarly treated and placed in a jar lined with black blotting paper. These were put side by side on my table. It was not possible to detect any effect whatsoever in the coloration as a result after two hours' test.

One of the specimens then had the toe disks clipped off with sharp scissors and was placed by itself in a jar. This operation very effectually inhibited the climbing power of the specimen, but at no time was there the slightest evidence that it involved any modification of the conditions affecting color.

A still more heroic experiment was made along the same line, viz., the section of the spinal cord after etherizing the specimen. It was closely watched to see what effect the process of etherization might have; but neither in the anesthesia, nor yet in the actual section of the cord was it possible to detect any color response. Later the entire cord was destroyed, but still without effect on color. This experiment was repeated at another time, but in a reverse order, viz., first a section of the sciatic nerve, later section of the cord, and finally the decapitation of the frog; but as before with absolutely negative results. In this case bits of skin from different regions of the body were placed in a damp jar along with living specimens to note what effect this might have as to the color of such detached bits. It was not possible to detect any certain evidence of direct color change, though after some hours, there was a *deadening* of the color such as one nearly always observes on recently dead frogs.

It must appear, therefore, more or less evident that these results are somewhat in conflict with those referred to by Lister and Biedermann. They seem likewise in conflict with results reported by Rogers ('06, p. 168), to the effect that section of the optic nerves resulted in a marked darkening of the skin. He found, however, that a color variety of the same species failed to respond in this manner. Carlton ('03 p. 267), found also that section of the cord in Anolis had little if any effect on its color changes, which agrees in the main with my own results. He argues, however, "Since it seems impossible to explain the conditions without assuming some nerves to be involved, and since the only other nerves present are the sympathetic, these observations point to the sympathetic fibres as the ones controlling the change from green to brown."

It has been a growing conviction with the writer that experiments of this character as tests of behavior in particular, and also reactions of many other sorts, are extremely untrustworthy at best. The very nature of the experiment,—the anesthesia, the operation, and the consequent shock all conspire to involve the organism as a whole in such physiological state as to render reactions more or less abnormal, or even pathological. But in any case there must be the greatest care to have results confirmed by the most positive evidence from natural sources. And until we have larger confirmation from such experiments than is at present available prudence will suggest caution in drawing sweeping conclusions.

Darkness and *Light.* As shown in the case of H. versicolor, and as noted by other observers, the effect of bright light is often to induce a lightening of the skin color in amphibia. In some cases this takes place rapidly, even in 10 minutes under the strong influence of heat and light. This was found to be more or less true in the case of H. arborea, though the time involved in reaction to light is usually gradual. But it must not be overlooked that exposure to direct sun often involves a higher temperature. In several cases this was found to vary as much as 10 degrees C. within half an hour. From what will be shown in the next section it may appear quite probable that some of the changes one might be disposed to attribute to light are really induced by heat. But even here there are very conflicting results. However, the sum of numerous experiments go to deepen the impression that the usual effect of light is to induce a lighter skin color.

But on the other hand, my experiments of a converse character, viz., touching the effects of *darkness*, do not show any converse darkening of color. Many experiments were made to test this, and for the most part with negative results. In many cases the test was made by using a dark hood which could be easily slipped over the jar rendering the interior very dark. Of course, all degrees of time enable one to be certain that a given condition had not been overlooked or escaped attention. Another method, already referred to, was to place the jars or cage in a cool dark room for any desired time. Here one could inspect the results after an hour, or after any number of hours. The results from both methods were to the same effect, viz., that darkness of itself, at least in my experiments, has no appreciable effect as to color changes in this species.

One of the very significant features of all these experiments was the marked discrepancies in results. For example, in one case a specimen was transferred from a dark jar into direct sunlight. During the first 15 minutes no color change was apparent; the specimen became very restless, moving about constantly, and soon the color began to darken, and in 15 minutes more had become almost black. This is but one of several such cases.

Temperature. It has been concluded from many observations that temperature is often a feature of marked importance. Parker has so held in relation to Anolis and Phrynosoma (op. cit.), and others likewise have drawn similar conclusions. As shown in experiments with *H. versicolor*, so with *H. arborea*, this factor seems not to be of large value in relation to color changes. My experiments with the latter species on this point were made by two modes, viz., first by subjecting the specimen to room temperatures of different degrees; second, by subjecting specimens to baths of different degrees. Both these were used with this species, but the latter was by far the more convincing. By this mode water of measured temperature was prepared and a specimen placed in it for certain definite time. In the first of these temperature tests some five specimens were tried. Four of these showed very evident lightening of color when subjected to a temperature of 30 to 35 degrees C. for 10 minutes. But a fifth specimen grew positively darker under the test and at 36 C. had become almost black. To make it perfectly sure that these results were not due to the water alone others were tested in a warm oven of the same temperature, and with essentially the same results. This curious effect may be noted, that there was marked individual difference as to the effect of high temperature; a given specimen showing no distress at a temperature of 35 degrees or even 36 degrees C., while another would actually collapse at 30 degrees. This was repeatedly shown, both in the bath and in the oven. In every case, however, removal from the bath was followed by rapid recovery, except in one case where some two hours was necessary for complete recovery.

Following the tests for high temperature there was a subjection of specimens to greatly lower temperature. For example, a specimen was taken from the 35 degree bath and placed in one of 10 to 12 degrees. In this reversal of the temperature there was, as in the case of darkness, an almost invariable negative, i.e., there was no tendency to induce a corresponding darkening of the color. It frequently happened that the light color would persist for from one to several hours, though in most cases the resumption of the original color followed in about an hour. But in any case it was quite evident that the cold bath showed no tendency to hasten the matter.

It was said above that exceptions were not wanting. One has already been mentioned which showed a directly contrary color change. This was also the case with one other specimen. It remains to mention the fact that still others failed absolutely to show any response whatsoever. They were first subjected to a temperature of 30°, then to one of 35°, and finally to a still higher, but under the ordeal they remained neutral, or with a slight darkening of color in one.

Here as in preceding experiments with light we have not only such individual differences as might be expected, but we have actually contradictory results, or what *seem* to be such. The question may arise, Are they *really* such? In the light of all the facts I am prepared to answer this query in the negative. Not only are they not contradictory, on the other hand they but emphasize afresh the conclusion elsewhere enunciated by the writer that we are here dealing with sentient, volitional individuals, whose behavior is involved in exceedingly complex nervous and physiological states, the nature of which we may hardly dare to guess. That they are creatures subject to varying stimuli every day, and meet them variously, may be accepted as a matter of course. That in response to the more common of these stimuli there comes about a general correspondence or agreement in behavior by experience and heredity may likewise be accepted as a general conclusion not open to serious debate. But that *all must show the same reactions all the while and under all circumstances*, whether in their native habitat or under the artificial conditions of a laboratory, only he whose intellectual horizon is bounded by the bias of preconception and theory will be likely to claim. These conflicting (so-called) aspects of behavior are the exceptional methods by which a given individual endeavors to meet an exceptional condition. Colors in a living creature may be fixed, as in the dead pigments of feather or hair, or they may be the expression of the complicated play of living cells or tissues. In some cases they have become in the course of phylogeny more or less adaptive; and in some they seem under individual control. That they should at times exhibit differences and peculiarities need excite no startling exclamations of surprise or incredulity.

Other experiments. Various other stimuli were made use of in the course of my studies. Among them may be mentioned a few dealing with the matter of physical irritation, such as pricking with a needle, pinching with forceps, etc. These were tried with both species and in each series with essentially similar results. In such an experiment the specimen would be placed in a shallow box or dish, and by using a sharp pencil or sometimes a needle it would be made to leap actively about for some time, in some instances almost to the point of exhaustion. In the case of *H. arborea* the specimens would often emit during such treatment the most plaintive little squeaks at each leap, or when sharply pinched. But while in some cases these stimuli would be associated with a definite darkening of the skin color, at other times it would have just the opposite effect, the color becoming just as evidently lighter.

It was the same in case one pinched the skin of body or leg with the forceps. Some would rapidly darken, others become lighter, and still in other cases not the slightest change. So too, in holding with the fingers or forceps while the creature struggled to escape, some would change color, others would show no response. The experiment was also tried of picking up a jar with specimens and moving it quickly, or roughly about, or even shaking it from side to side; and here again with similar results. In these respects the behavior of *H. versicolor* and *H. arborea* show a very marked similarity, as in other points already referred to.

Still other experiments were made but they add nothing essential to those already described and need not cumber the pages further. Compared with the accounts given by others (vide supra), these may seem somewhat inconclusive; and but for those relating to *H. versicolor* they would be so to the writer. However, they are what they are,—facts to be reckoned with; and as such are submitted for the consideration of any who may be concerned with them. It may be worth while to merely mention the observation of Meyer, cited by Biedermann (op. cit., p. 489), to the effect that certain frogs (*H. temporaria*) are more responsive in reactions to light during fall and winter than in spring. "Wenigstens bleiben in dieser Jahrzeit die Thiere haufig im Licht dunkel, im Finstern hell." I cannot believe, however, this can be of importance so far as the general facts are concerned.

Psychology of Behavior. It is no part of my present purpose to enter upon a discussion of the intricacies of this feature of behavior, but merely to suggest a very few points in connection with certain aspects which have been submitted in earlier sections of the paper. Attention has already been directed to the fact that frogs must be regarded as having small claims to intelligence, and after one has had various species under observation for some time this verdict is not likely to be greatly modified. While it is true that frogs have succeeded about as well as the average of their class, and indeed better than most, if one may judge from the number of either species or individuals, still this has come about more by virtue of the peculiar instincts and habits than by the degree of intelligence which has been involved. However, one must not lose sight of such facts as are clearly indicative of intelligence. Both by observation and experiment it has been shown over and over again that frogs are capable of learning, they have memory, they profit by experience, etc. (cf. Yerkes, Instincts, Habits and Reactions of Frogs. *Harv. Psy. Stud.*, vol. I, 1903; Holmes, Biology of the Frog, Chap. XIX, 1907).

But, as already intimated, it is not my purpose to consider this aspect of the problem. I have been concerned in observing the very apparent association of emotional, and other neurological phenomena in connection with behavior. This was especially marked in certain cases of color change associated with handling, or close scrutiny. What was at first thought might be a direct reaction from darkness, as in the carrying of specimens in dark boxes, etc., was later found to be probably an emotional or nervous reaction due to handling. And the same was found to be the case in certain instances where specimens became aware of the fact that they were under observation. This happened too often to be regarded as merely a coincidence. And it seems altogether probable that some of the *apparent* conflicts of behavior are likewise due to psychic or emotional factors. Gadow cites cases in which male lizards while fighting exhibited marked color changes. And the facts herein described seem, at least in certain cases, to find their simplest explanations just along these lines.

In our zeal to interpret every aspect of behavior in terms of chemistry, or physics, impelled by a blind adherence to the law of parsimony, the tendency has been to proscribe any appeal to the psychical and to hold up to some measure of contempt any disregard of this rule or method. Far be it from me to invoke the mystical, or to read into animal activities a hasty anthropomorphism; yet as I have had occasion to point out in another connection, it is more than possible, indeed highly probable, that under the current stress of a *scientific fashion* not a little of current interpretation has been vitiated by the folly of a blind following of blind adherence to theory. He is a rash leader who would fix the metes and bounds of consciousness or mind in the world of the living. Surely it is no longer circumscribed by the genus Homo! If the first limit set at this point was by a procrustean *philosophy*, let us beware that the onus of a similar, not to say worse, blunder be not laid to the charge of a hasty *science*! There are other minds than ours, and they share something in common with us in those psychic powers which count for something in the stress of evolution, and as behavior in its manifold aspects gives expression to the endless struggle it is not strange to find involved therein the psychic along with other factors which go to constitute the organism and its environment.

SUMMARY

1. The species of tree frogs herein reviewed show on the average a lightening of skin color in the presence of strong light, but with marked exceptions.

2. Darkness has not been found to have any appreciable effect in relation to color changes.

3. A high temperature seems to act much as strong light to induce a proximal migration of chromatophores, hence to produce a lightening of skin color; but as in 1, with marked exceptions.

4. A low temperature has not been found to have any direct effect as to color changes.

5. It has not been found that the nature of contact stimuli has had any appreciable influence on color changes.

6. Color changes of these species of *Hyla* seems largely under nervous control. Various emotional and perhaps other psychical factors appear to be dominant in the behavior above considered.

As a final word I desire to express my obligations to the Director and Staff of the Naples Zoological Station for courtesies extended to me, and also to the Secretary of the Smithsonian Institution for the courtesy of an appointment to its table at this renowned laboratory.

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NOTES

A CASE OF INSTINCT

A young sparrow hawk fell out of its nest in the broken cornice of one of the college buildings and was brought to my office. I took it home and put it in a wire cage, set on a large stone at one side of the lawn, where it remained for two months. The first meal I gave it was of fish worms which I dropped into its mouth. The second day I fed it cooked liver cut into small bits, which I placed in its mouth. On the third day I placed a piece of roast beef half the size of an egg on the bottom of the cage. The hawk looked somewhat cautiously and then thrust out one foot and grabbed the meat, viciously sinking his claws into it. Its feathers ruffled, it spread its wings and fluttered about the cage still holding the piece of meat which it continued to strike with its bill, its other foot and its wings. With its outstretched wings, its curved back, its ruffled feathers and its savage thrusts with beak and claw, it seemed a much more formidable creature than it had when swinging on the swing a moment before. The transformation from the sleek, handsome, open-eyed bird to the infuriated beast was so sudden and complete as to be really startling. One could well imagine that such behavior would be effective in intimidating any small creature such as mouse or bird that might be so unfortunate as to fall its prey. Under the circumstances it seemed quite useless behavior in view of the already docile character of the roast beef.

I continued to feed the hawk on some form of cooked meat and the food always elicited the same sort of behavior. The extent of the demonstration seemed to depend somewhat on the hunger of the bird and the size of the piece of meat, great hunger and a large piece producing the more exaggerated behavior.

Since the hawk was evidently too young to fly when brought to me, it seems improbable that it had ever killed any animal or that it had ever witnessed such killing. If this is true we have here a clear case of the congenital tendency to kill prey. Whether one could analyze the hawk's behavior into that concerned directly with the act of killing and in addition certain elements of behavior which could only be useful in intimidating the prey I am not sure. I am inclined to think that such an analysis could be made. That the instinct is not absolutely rigid is evidenced by the fact that the stimulus lacked most of the characteristics that the normal stimulus would have. There was no movement, no feathers, no hair, no odor of living animal. It may have been the odor of the meat, for bread did not stimulate the behavior, nor did any other kind of food even though it was dark like the meat.

The hawk was quite tame from the start and I could handle it with impunity. Only once did I find out the razor-like quality of its beak and claws and that was when in changing it from one cage to another I hurt its wing. The dogs nosed about the edges of its cage but it was never frightened by them nor did it show any disposition to attack them.

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